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BIOLOGY AND CONTROL

of the

WESTERN PINE BEETLE

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BIOLOGY AND CONTROL

of the

WESTERN PINE BEETLE

A Summary of the First Fifty Years of Research

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U.S. Department of Agriculture

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NOTE: John A. Miller, senior author, died April 1952 while actively engaged in research on forest insects with the Food and Agriculture Organization in Mexico City. F. P. Keen, junior author, retired from Government service in December 1955 but has remained with the Forest Service as Collaborator.

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INTRODUCTION

The western pine beetle (*Dendroctonus brevicomis* Lec.) has been the subject of more intensive study by forest entomologists and foresters during the past 50 years than any other western forest insect. It has, in fact, been the center of a group of entomological studies—of the beetle itself, of associated insects, and of certain factors that enter into the ecology and management of ponderosa pine stands. This attention is due both to the importance of the beetle as an enemy of ponderosa pine and to its capacity to destroy large volumes of valuable timber that would otherwise be available for utilization.

This beetle undoubtedly was a factor in the ecology of ponderosa pine stands long before it became known to science. Pine stands that approached maturity were thinned by beetle epidemics, and new trees grew up to replace those that were killed. But, as long as Indians used the forest only for hunting grounds and the first white men were interested only in trapping and livestock ranching, no one cared what happened to the trees. The beetle was of no economic importance until the advent of the lumber industry.

Then, as the realization developed that the supply of virgin pine stumpage was limited and that the beetle was hastening exhaustion of the old stands, the western pine beetle became a problem of great importance. The beetle upset logging programs and shortened the life of sawmill communities because it often became active in the woods before loggers reached the timber. It killed the very trees that the lumberman preferred to cut and mill into high-quality lumber. Its work earned it the epithet "The Pine Beetle Logging Company" (*86*).

Timber values destroyed by the beetle fluctuated with stumpage prices in different periods and regions, but the economic loss can be visualized in terms of the board-foot volume of timber killed annually. For the ponderosa pine region of the Western United States, the total annual loss from the western pine beetle during the past 50-year period has varied from about 500 million to 3,500 million board feet. The average annual loss has been estimated at about 1 billion board feet. If this stumpage had been manufactured into lumber, it would have supplied sawmills employing 57,000 people with an annual payroll of $18 million. The lumber would have produced enough material to build 100,000 5-room houses. This is a tremendous loss for western timber industries and the national economy to absorb year after year.

Investigations of the biology and control of the western pine beetle began in 1900. Since 1902 continuing studies have been conducted by the Division of Forest Insect Investigations of the Bureau of Entomology (reorganized as the Bureau of Entomology and Plant Quarantine in 1934), U.S. Department of Agriculture. In December 1953, the Division was transferred to the Forest Service, Branch of Research, and became the Division of Forest Insect Research.

Many investigators in several localities of the western pine region have contributed to a steadily accumulating fund of information on the western pine beetle. Much is known about the life history and behavior of this beetle, its role in pine stands, and what can be done to control or prevent the waste of timber that it causes. Surprisingly little of this information has been published. The great bulk of the results of western pine beetle research is in manuscript reports filed in the Division of Forest Insect Research and accessible to only a few forest entomologists. Thus there has existed a definite need to extract, summarize, and publish the essential information in these reports.

This publication reviews the results of research on the western pine beetle up to July 1, 1952. It shows the progress that has been made in over a half-century of study of this one bark beetle. It also records the trials and errors—the research that ran into blind alleys. The record of this pioneer effort in the field of forest entomology in the United States should be of great help to research workers who are faced with similar problems.

Primarily the text is intended as a reference for research workers and for fieldmen concerned with surveys, the appraisal of infestations, and control. The more important results of past work are abstracted or quoted from published papers and from manuscript reports; some interpretation has been given to the results when this seemed desirable. Even though several of these papers and reports show dates later than 1952, the research work was largely completed before that time.

SECTION I. BIOLOGY, SEASONAL HISTORY, AND HABITS

GENERAL

Taxonomy

The original description of the western pine beetle published by Le Conte (*83, p. 386*) [1] was of a single specimen from middle California. Although this description has been somewhat modified by other taxonomists from study of larger series of specimens, the validity of the species has apparently never been questioned. Hopkins (*43*) states that Le Conte's type was a male and that the description agrees with the specimen "except that the prothorax is not nearly twice as broad as long." He gives a full technical description of typical females and males.

Swaine (*132*) gives the following brief technical description of the adults:

> Length, 3.2 mm. to 5 mm., average 4.2 mm.; colour dark brown to black; the front elevated on each side of a deep median groove in the male, faintly so in the female; sides of the epistomal process oblique; the pronotum shining, *hardly constricted in front*, feebly so in the male; the *elytra as wide as the pronotum;* the striae faintly impressed, the strial punctures very small, the discal interspaces *densely, finely* asperate, the declivital striae faint; broadly impressed on each side of the elevated suture; *the pubescence rather abundant, everywhere short, erect,* and *inconspicuous,* with a few slightly longer hairs intermixed on the declivity. The female has a narrow, transverse elevation across the pronotum behind the cephalic margin, continued across the sides; the male has a transverse depression similarly situated.

Hopkins (*44*) gives the following brief general description:

> The western pine beetle is a rather stout, brownish, cylindrical bark beetle, from 3 to 5 mm. in length, with head broad and grooved, pronotum punctured and but slightly narrowed toward the head, and elytra with fine rugosites, but entirely without long hairs.

Very closely allied to the western pine beetle is the southwestern pine beetle (*Dendroctonus barberi* Hopk.). It attacks ponderosa pine in Arizona and New Mexico but does not overlap the distribution of the western pine beetle. For the layman these two species are difficult to distinguish, but according to Hopkins (*43*) the southwestern pine beetle can be distinguished by "the prevailing coarser regosites of the elytral interspaces and the distinctly impressed striae." Swaine (*132*) confirms this character for the separation of the two species.

For purposes of identification in the field, the egg galleries cut by beetles in the inner bark provide a reliable character for distinguishing the work of the western pine beetle from that of other scolytids within its range. These egg galleries, which will be de-

[1] Italic numbers in parentheses refer to Literature Cited, p. 355.

scribed later, form a winding, crisscross pattern unlike that of any other species of bark beetle with which it is associated. The egg galleries of the southwestern pine beetle are very similar except that, according to Hopkins, they are "usually distinctly transversely winding," instead of "subtransversely winding" (*77*).

Host Trees

It is well established that the western pine beetle is highly specific in its host selection. Four tree species appear in the host records, but two of these can be considered as accidental.

Pinus ponderosa Laws.—Western yellow pine was first listed as a preferred host by Hopkins (*43*, *44*), and all subsequent publications agree in placing this tree species first as the selected host of the beetle. In March 1932, the common name of this tree was changed to ponderosa pine, and it is so designated throughout most of this text. The earlier name of western yellow pine appears in some early quotations.

Pinus coulteri D. Don.—Unpublished notes in the files of the Forest Insect Laboratory at Berkeley reveal that the beetle was first collected from Coulter pine in 1915 near Julian, Calif., by F. P. Keen. Specimens sent to Dr. A. D. Hopkins at that time were tentatively identified as the southwestern pine beetle. Later Hopkins made a careful study of these specimens and changed the determination to the western pine beetle. Throughout southern California, the western pine beetle's preference is equal for Coulter and ponderosa pine.

Pinus lambertiana Dougl.—Hopkins (*43*, *44*) records the occurrence of the western pine beetle in sugar pine, but this record was questioned soon after the first detailed investigations were started in the West. Hopkins' original notes indicate that the beetle was found in what was considered to be a sugar pine log at a mill near Grants Pass, Oreg., but there was some uncertainty as to the tree species from which the log came. Continued observations by other workers extending over many years have failed to record any attacks on sugar pine under normal forest conditions. According to Miller (*U177*)[2] experiments to force attack by the beetle on sugar pine logs in cages resulted in the beetles entering the bark and extending short egg galleries, but no broods developed.

Pinus contorta Dougl.—An attack on lodgepole pine under natural conditions near Bly, Oreg., was reported by Keen (*63*, *64*). It occurred where lodgepole was growing in proximity to heavy-grouping attack by the beetle on ponderosa pine, and it seems to have been due to an overflow of population. In one case there was evidence of successful brood development in lodgepole. Chamberlin (*19*) also mentions lodgepole pine as an accidental host of the western pine beetle.

Distribution

Hopkins (*43*, *44*) lists localities in California, Oregon, Washington, and Idaho where the beetle was collected before 1909. Keen (*75*, *p. 132*) states: "The western pine beetle is the most important

[2] Italic numbers in parentheses preceded by the letter "*U*" refer to Unpublished Manuscript Reports, p. 363.

insect enemy of ponderosa and Coulter pine within the range of these trees from Baja California north into Oregon, Washington, Idaho, Montana, and western Canada." The species has not been collected in Baja California, nor east of the Continental Divide in Montana. It is associated with the Pacific coast form of *Pinus ponderosa* and is not found in *P. ponderosa* var. *scopulorum* through the Rocky Mountain range of this variety (fig. 1). The beetle's near relative, the southwestern pine beetle, is found in the southwestern pine region of Arizona and New Mexico.

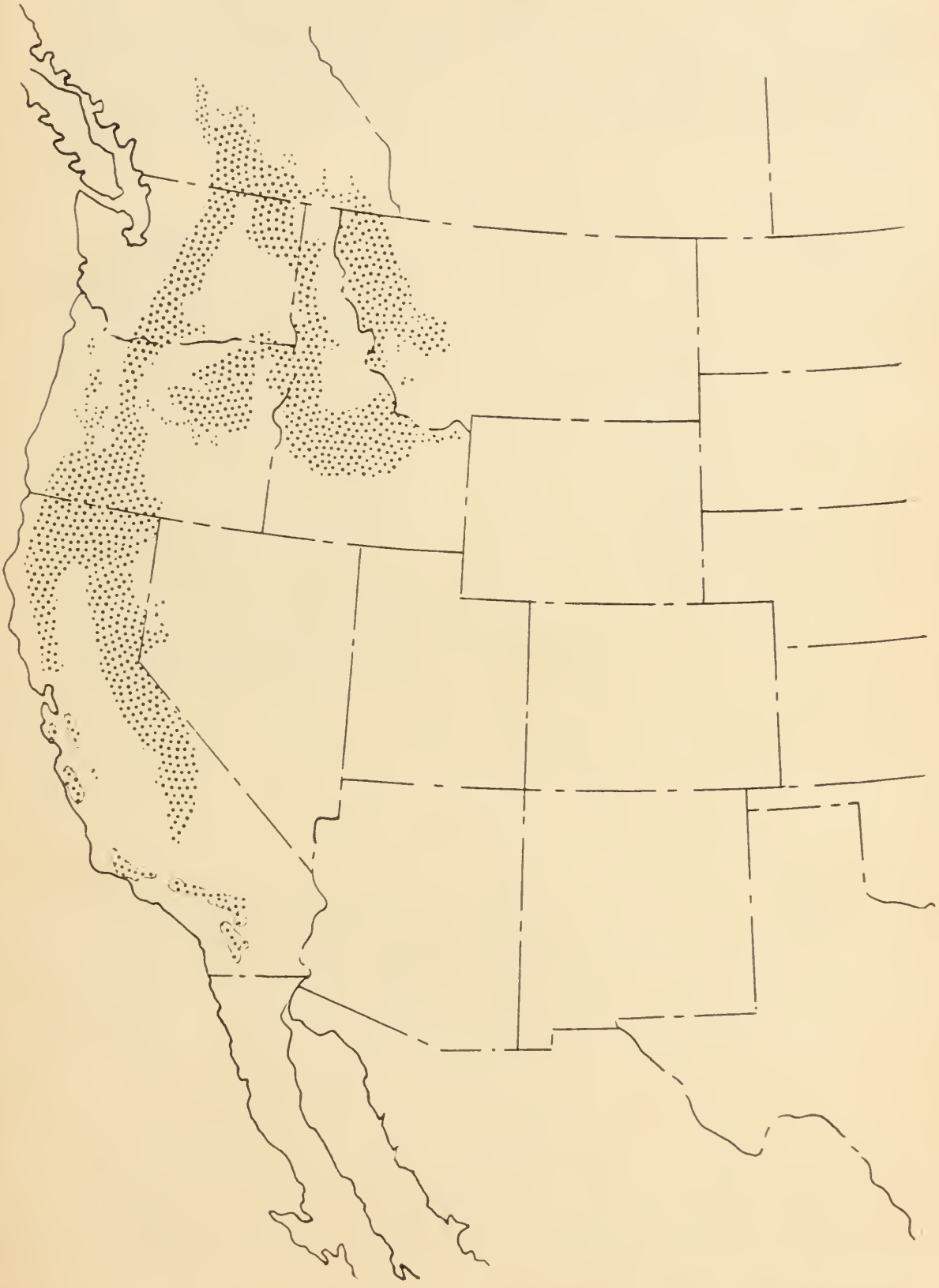

FIGURE 1.—Distribution of the western pine beetle (*Dendroctonus brevicomis* Lec.) in western North America.

LIFE HISTORY

The life history of a western pine beetle can be considered to begin with egg, which is deposited by the parent female beetle alongside the egg gallery in the inner bark of a pine tree. When the eggs hatch, the young larvae feed for a time by boring a tiny mine in the inner bark. They then turn outward and enter the outer bark to complete feeding and to mature. The final activity of the larval stage is to enlarge the mine in the outer bark into a cell in which pupation and transformation to the adult stage take place. During all this period of feeding, growth, and development, there are many hazards and brood mortality is high.

Those larvae that succeed in completing their development and survive the transformation as pupae reach the adult stage. From this point on the adult passes through a series of activities that make up the life of a beetle—emergence from the tree in which it has been reared, a period of flight, attack upon another tree, mating, egg gallery construction, oviposition, re-emergence, and possibly attack upon another tree—until the beetle finally dies. It usually dies at the end of one of its egg galleries, unless it meets with some fatal accident sooner.

It is necessary to select one of the four stages in the life cycle of the insect (fig. 2) to begin a review of the accumulated information on its life history. It would seem logical to begin with the egg stage, but the decision is complicated by the fact that the egg first begins in the body of the parent beetle and the place where it starts incubation is determined by the activities of the adult just before oviposition. Consequently, it seems best to start with the adult beetle.

The Adult Beetle

Individual beetles, even after becoming fully mature, vary appreciably in size and color. LeConte described the type male as "red-brown." Hopkins stated the color variously as "light brown" or as "brownish to nearly black." Swaine says they are "dark brown to black." Adults are light brown if not fully mature, but gradually darken to brown or nearly black.

The relative size of the beetle has been given some special attention because it was believed that this was an indication of adequate nutrition during the development of the brood. Hopkins gives the length as 3 mm. to 5 mm. In 1941 Yuill (*U346*) compared the size of adults emerging from high-risk trees with those from low-risk trees, using weight as an index. On the basis of 2,790 newly emerged adults, he found that those from high-risk trees average 6.2 mgs. per beetle, while those from low-risk trees averaged 4.0 mgs.

Further measurements of length were made by R. C. Hall and C. Startt at the Hat Creek Field Station (California) in 1942. Their findings, recorded only in field notes, showed a range in beetle size from 3.1 mm. to 5.2 mm.; 500 males averaged 4.15 mm., while a similar number of females averaged 4.38 mm.

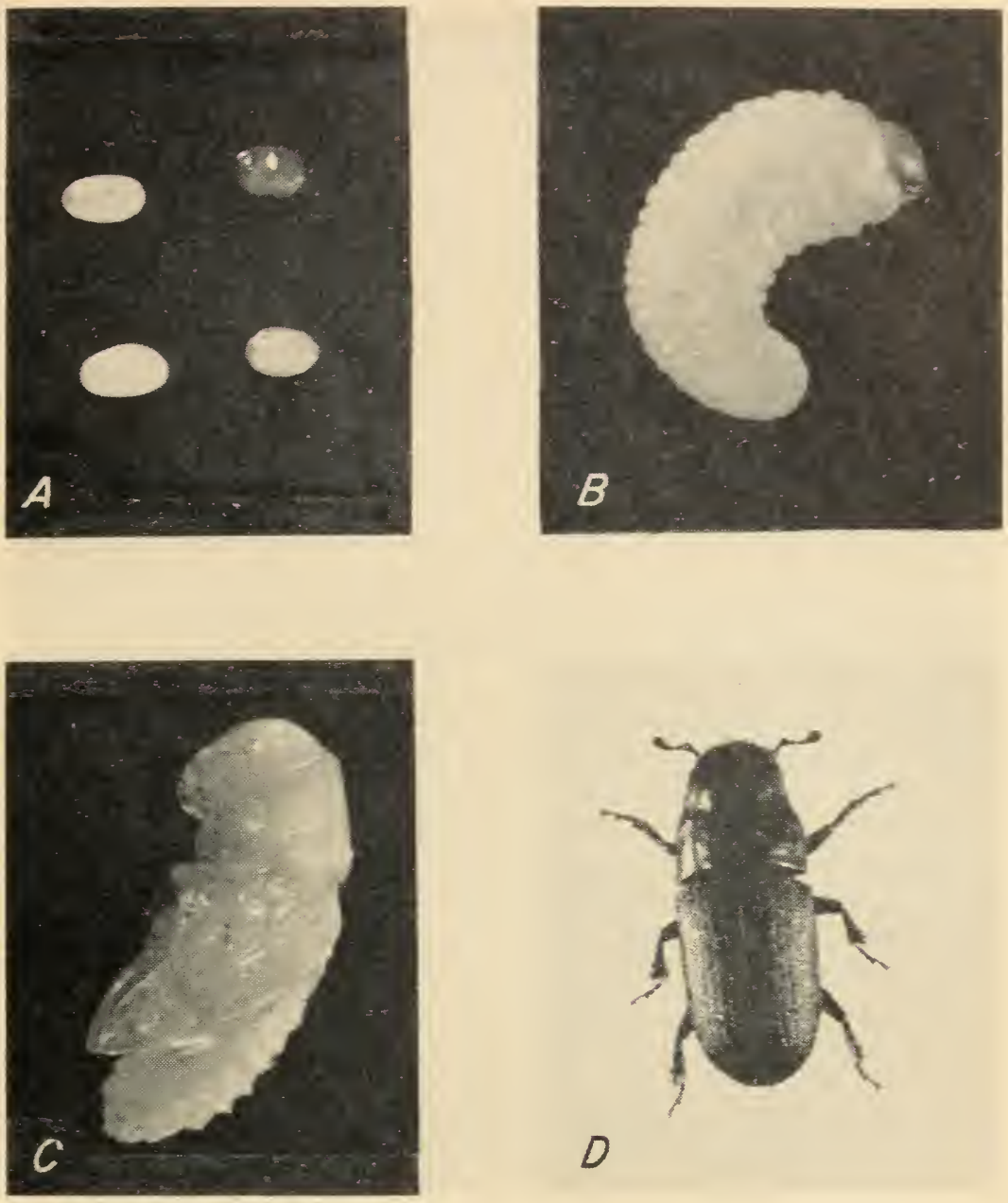

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FIGURE 2.—The four stages of western pine beetle (*Dendroctonus brevicomis* Lec.) : *A*, Eggs ; *B*, larva ; *C*, pupa ; *D*, adult. ×8.

Ratio of the Sexes

Few studies of sex ratios have been made, but they indicate an unequal distribution of males and females. In the first Ashland studies, Keen (*U130*) made sex determinations from some 428 emerging adults and also from the adults collected from 66 new attacks. It was found that "Females, both in emerging and attacking, outnumber the males by a ratio of 54 to 46. Polygamy is found to occur."

Life Duration of the Adult

The question of how long the adults may live, both before and after they make their attack on a tree, has been given little study except in the biological investigations at Ashland, Oreg., in 1916. From a summary of records on parent adults in 14 trees attacked in the fall of 1915, Keen (*U130*) found that "the average life of

parent adults overwintering in the tree [is] . . . 214 days or about 244 days total life (including an estimate of 30 days from the time beetles first form until trees are attacked. The maximum (life) is a total of 270 days." When deprived of their normal food supply by being kept in a glass tube with a cotton stopper, both parent adults and new adults "died within about 15 days." These parent adults in a winter brood tree went through the colder winter months in a dormant condition. This period of arrested metabolism undoubtedly extended the duration of life much longer than that of continuously active parent adults.

Food Habits

It can be assumed that in order for the beetles to live as long as these observations indicate, the adults must feed. The fact that they die rather quickly if confined where no food is available is further proof of this point. Keen (*U130*) studied the matter of food habits and concluded that: "It was not definitely determined whether the adults feed while constructing their galleries, but they probably do. The major portion of the frass in the galleries is made up of small pieces of wood cut out of the gallery and placed to one side." It was not until 1929 that the food requirements of the adult became a subject of detailed investigation. The studies were stimulated by the possibility of finding attrahents that could be used in trapping beetles as a control method; a search was made for the materials in ponderosa pine that make certain trees especially attractive to the beetles.

Struble (*U294*) studied the material found in the alimentary tract of the beetle and conducted a series of experiments to determine when the beetle feeds and what parts of the tree are used as food. It was thought that the adults, like some other beetles that breed in the cambium, might feed on pine foliage or other plants during the flight period. For instance, adult species of a related genus, *Phloeosinus*, feed in twigs of their cedar host plants before they attack the main bole and oviposit. Also, the pine flatheaded borer (*Melanophila californica* Van Dyke) is known to feed on pine foliage before it oviposits on the tree.

Struble found that the western pine beetle ingested outer bark into the alimentary tract before it emerged, and inner bark while constructing egg galleries. He also found a yeast present in the digestive tract of the beetle which actively inoculates the inner bark tissues when the beetle enters a living tree. Struble's conclusions were (1) the beetles feed continuously during the time they are in the bark (outer) prior to exit and while they are extending their egg galleries. (2) Adults do not feed on needles or twigs of yellow pine. (3) A yeast is definitely associated in the digestive tract.

In 1930 Jeffrey (*U108*) followed up these nutritional studies, giving particular attention to the biochemistry of the inner and outer bark ingested by adult beetles. He summarized their feeding habits as follows:

Period:	*Material ingested*
First day or two (after pupal stage)	None.
During emergence	Outer bark.
During flight	None.
While entering tree	Outer bark.
While constructing galleries	Inner bark.

His chemical analyses of the inner and outer bark indicate that these contain sufficient sugars and starches in available form to provide nutrition for adult beetles. Although considerable attention was given to the availability of food materials for larval broods, no further observations were made of the feeding habits of adults.

The Attack

The method of attacking a tree is one phase of the beetle's activity that can be closely observed, and it has been described in several reports. In describing the attack, Webb (*144*) stated:

> Large numbers of the beetles usually settle upon a few trees close together and crawl about upon the bark from near the base to about two-thirds of the distance to the tree's top seeking suitable places for entrance. Crevices in the bark are favorite places . . .

After observing the attack on a series of trees near Ashland, Oreg., in 1915–16, Keen (*U130*) recorded the following:

> A female was observed to alight on a log and after 5 minutes of walking around and examining it, started boring into a crevice within 6 inches of where she lit.
>
> There appears to be no sudden or concerted attack on the part of the beetles, but rather a slow continuous attack depending upon the abundance of the beetles striking the tree at some weak point near the top and then gradually extending the attack down the trunk until resistance of the tree is gradually overcome.

Person (*U238*) described the initial phases of an attack which he followed in 1926:

> Flight to the tree started shortly after sunrise and continued until about sunset. The flight is spasmodic. A number of *D.b.* [*Dendroctonus brevicomis*] would fly to the tree and when they became quite abundant, a number of *Enoclerus lecontei* (*Thanasimus nigriventris*) would appear both by flight and by crawling from other parts of the tree. This would cause the *D.b.* to hide in bark crevices and under the bark scales or drop to the ground. Then in a short while the *T. nigriventris* would disperse and another group of *D.b.* would fly to the tree. This would continue throughout the day during the entire period of flight to this tree if weather conditions were favorable. Between 8:30 A.M. and 9 A.M. on May 14, a total of 14 *D.b.* flew to this tree and lit inside of a bark area of about 6 square feet. This is about as heavy a flight as was observed during the season. Some of the beetles held onto the bark where they lit while others fell to the ground.

Character of Bark Selected for Attack

As the beetles attack a tree to which they have been attracted, they normally select bark areas that have formed the corky layers of the outer bark; the young thin bark on the upper bole and limbs is usually avoided. Consequently a diameter of from 4 to 8 inches usually marks the upper limit of infestation. The limbs of large

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pines are rarely attacked and then only when their bark surface has aged to the point of forming cork plates. Young trees from 6 to 8 inches in basal diameter are rarely attacked by the western pine beetle.

One explanation for this selective habit may be found in the fact that as the larvae develop they complete their feeding and transformation in the corky layers of the outer bark. The adult, therefore, in selecting the place for oviposition avoids the younger trees and those parts of older trees which do not provide outer-bark medium for the later stage of brood development.

Location of First Attacks

Usually the first attacks are made in the upper midbole and then progress up and down the trunk to include all of the corky bark area. The basal few feet of the stem, which retain moisture in the bark and sapwood the longest, are the last to be attacked, or may be ignored entirely.

Density of Attack

Beetles seem instinctively to distribute their attacks so that overcrowding does not occur in any particular bark area. After a certain number of beetles have started their attacks within a square foot, later arrivals seek entrance in bark surfaces not already occupied. This habit is necessary in order to ensure adequate food supply for the larval broods. Although many pairs of beetles could easily attack the same square foot of bark and construct egg galleries, larval broods developing under such conditions would exhaust their food supply before they became full grown and thus be doomed to starvation. Consequently the beetles seldom carry the density of attack to the point of overstocking the bark. The number of attacks per square foot of bark varies considerably, but always remains within certain limits.

Person (*U238*) found a difference in density of attack between trees attacked by first-generation beetles in the spring and early summer and trees attacked by second-generation beetles after the seasonal growth period had subsided: First-generation beetles counted on 193 square feet—average attack per square foot, 14.3; second-generation beetles counted on 184 square feet—average attack, 10.0.

Where large populations have built up and the beetles are forced to attack trees of more vigorous growth rate, the density of attack has been found to increase. Miller (*93*) reported that 20.6 beetles per square foot attacked standing trees after emerging from windfalls in 1921.

> The attacks within the bark were so numerous that there was not enough food to supply all the developing broods; as a result the emergence (following these attacks) was only half the normal . . .

Patterson (*U218*) and Miller (*U191*) recorded the attacks per square foot from over 2,300 square feet of infested bark collected in southern Oregon and central California (fig. 3). In 1928 Keen (*U142*) summarized and analyzed statistically all the information on beetle populations that had been accumulated by different ob-

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FIGURE 3.—Paper tags show density of western pine beetle attack on lower bole of ponderosa pine.

servers up to that time. He found averages that ranged from 5.5 to 21.6 attacks per square foot. The general average for a total of 4,177 square feet of infested bark was 11.6 attacks per square foot.

Duration of the Attack

When a tree is successfully attacked, the beetles keep coming until they have overcome its resistance and occupied most of the selected bark surface. The length of this period varies a good deal. Keen (*U130*) describes an attack which lasted from April 25 to July 3 on the same tree, beginning in the upper bole and extending gradually to the base. In another tree the attack lasted from March 11 to May 4. This type of attack was found to be typical of a great number of trees on areas near Ashland, Oreg., in 1915. However, Keen states that "during the height of the attacking period, some trees were attacked so rapidly that it is as though they were attacked simultaneously throughout their length."

Person (*U238*) records the period from the first attack until the tree was overcome for four trees in the Central Sierra of California in 1926. The attack on the base of these trees was forced by caging, but the main attack came above the cages from flying beetles. One of these trees survived from April 29 to May 20, a period of 21 days, before it was overcome; another was killed in 7 days and the other two were killed in 9 days.

It can be concluded that the period of attack varies with the number of beetles flying in the area. Under epidemic conditions attacks occur in great force and most of the trees are killed within 7 to 10 days. When the beetle population is light, attacks may be greatly prolonged.

Another factor that may prolong the period of attack is the resistance of vigorous trees. Person (*U238*) states: "The period between first attack and the date on which the tree was overcome was over twice as long for the fast growing tree."

Group Attacks

The first beetles starting an atack are nearly always attracted to a particular tree. If it is overcome and still other beetles are attracted to it, they do not attempt to occupy all of its bark but begin an attack on an adjacent tree. When the bark of the second tree is occupied, another nearby tree will be attacked; if the beetles keep coming, a group of attacked trees builds up around the initial center of attraction. Under highly epidemic conditions, a group may include as many as 200 trees, but ordinarily from 3 to 15 trees will absorb the force of attacking beetles drawn to any one center. A "key" tree, the one selected for the initial attack, can be found in almost all groups. Endemic conditions are marked by the attacks being limited mostly to single trees.

Sex Making the Initial Attack

Webb (*144*), Keen (*U130*), and Person (*U238*) all made observations which showed definitely that the female starts the attack. She finds a suitable spot in a crevice of bark and bores almost directly

into the phloem. About the time she reaches the phloem she is joined by the male who assists by pushing the excavated frass out of the entrance hole. The female continues the gallery and is followed by the male, who has never been observed doing any excavating but does help by working the pitch away from the entrance. One observer noted that the male does not even appear until the pitch starts to flow.

Mating Habits and Number of Beetles Per Attack

According to Keen (*U130*) females in flight and those found just entering a tree cannot produce fertile eggs in trap logs from which males are excluded. Only after the female has been joined by a male in the entrance chamber do the eggs become fertile. From this observation Keen concluded that copulation takes place in trees and not during the flight period. There are no records of copulation having been actually observed, which supports the theory that fertilization takes place after the beetles enter the bark.

Keen (*U130*) found some evidence of what he considered to represent polygamous relation: On 20 square feet of bark of one newly attacked tree, 66 attacks were noted with a total of 171 parent adults or 2.6 beetles per attack. Of these, "11 attacks were found containing 3 beetles each, of which 2 were females and 1 was a male." The beetles subsequently emerging from this tree were 54 percent female and 46 percent male. "In these polygamous galleries, sometimes the two females were found in the lead, one at the extreme end doing the construction work, the second female about 1 inch behind, and the male 2 or more inches in the rear of the last female. In other cases the male was found in the middle of the gallery with one female in the lead and one behind him nearer the entrance."

From an examination of 29 square feet of bark on the North Fork, Calif., area, Person (*U238*) reports finding an average of 12 attacks per square foot, but only two beetles with each attack. Patterson (*U218*) reported that 304 adults in 133 attacks were counted by an observer in the Ashland, Oreg., area. The number of beetles recorded per attack ranged from 1 to 5 and averaged 2.3.

Pitch Tubes

Formation of pitch tubes on the outer surface of the bark soon after the attack starts is described by Webb (*144*).

> As the first incision is made into the living inner bark, the tree begins exuding pitch to cover the wound made by the intruding beetle. This pitch or resin collects at the mouth of the entrance hole in the form usually known as a pitch tube. Where the attacking force of beetles is small, the efforts of the tree to heal these wounds not infrequently succeed, the flow of pitch being so great as to overcome and suffocate the beetles. . . . Where the attacking force is large, however, the flow of pitch does not seriously hinder the beetles.

The number of pitch tubes will usually indicate the number of beetles attempting to attack. The size of the pitch tubes is most

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FIGURE 4.—Pitch tubes in bark crevices may be evidence of attacks by the western pine beetle on a ponderosa pine.

frequently evidence of the magnitude of tree resistance. Highly resistant trees produce large pitch tubes, often with unsuccessful beetle attacks (fig. 4), whereas trees of low resistance often produce small tubes scarcely visible in crevices of the outer bark.

The Egg Galleries

As a tree weakens and succumbs to an attack, the resin flow ceases and the beetles extend their egg galleries through the inner bark. These are winding tunnels a little larger than the diameter of the beetle. Hopkins (*43*) describes them tersely as "sub-transversely winding." The gallery very lightly grooves the surface of the sapwood, and it is visible, after the bark is removed owing to stains left by resins. Jeffrey (*U108*) states: "These galleries penetrate the cambium and inner living bark. When a choice is possible, the gallery is closer to the cambium side of the inner bark where the cell walls are not very thick."

The parent adults keep several inches of the terminal end of the gallery, where they are working, free of frass. Frass is carried back and packed in the completed gallery behind them. Surplus frass that cannot be packed into the tunnel is dumped out to the

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FIGURE 5.—Bark removed from a ponderosa pine killed by the western pine beetle exposes winding, crisscrossing egg galleries in the sapwood.

bark surface through occasional adits cut through to the surface. These openings are known as ventilation holes. The galleries form a network in the inner bark, crossing and recrossing each other in a pattern peculiar to this species (fig. 5).

Noise of Construction

The chewing of the bark and wood by a great number of beetles extending their galleries is faintly audible. Keen (*U130*) states:

> They produce a faint crackling sound like the crushing of dried leaves; a noise very similar, only more continuous and not as loud, as that made by cerambycid larvas when gnawing wood. In several instances, attention has been directed to infested trees which showed no outward sign of insect infestation through noise made by attacking beetles.

In following an attack near North Fork, Calif., in 1925 Miller (*U193*) recorded:

> Noise made by the adult beetles in cutting their galleries could be heard. This noise was noted after 8 P.M. and before 6 A.M. as

well as during the day, indicating that the activity within the tree does not die down at night.

Rate of Construction of Egg Galleries

The only record on rate of gallery construction was made by Keen (*U130*) in the Ashland, Oreg., studies. He observed on caged logs that in June the female was able to construct an average of 0.65 inch of egg gallery per day; also that a ventilation hole is constructed for about every 4 inches of egg gallery. This is probably the maximum rate of construction under favorable temperature conditions. It is known that the construction of egg galleries ceases with the advent of cold weather in the fall. Since adult beetles become inactive at temperatures of 50° F. and lower, it can be expected that all activities connected with an attack slow down as the temperature approaches this point.

Position and Number of Egg Niches

After the female has extended the egg gallery a few inches from the entrance chamber, she begins to make tiny notches at frequent intervals along the sides of the gallery to receive the eggs. The notches have been described by Keen (*U130*):

> The egg niches are located in the soft bark off the main gallery and separated from it by a wad of frass which is packed into the niches after the egg is deposited. Often when the bark is stripped from the wood, the eggs are visible in their niches, but more often they are concealed by the frass packing or a very thin layer of the phloem. The number and distance apart of the egg niches varies greatly with the different attacks and even in the same egg gallery being very irregular. Sometimes the eggs are only one-sixteenth of an inch apart and at other times there will be 3 or 4 inches of gallery with no eggs on either side.

From an examination of 210 inches of gallery representing 11 attacks counted on 11 trees, 591 eggs were found—an average of 2.8 eggs per inch of gallery.

Person (*U238*) examined 19 square feet of bark on 13 trees and counted 5,693 eggs in 1,363 inches of gallery or an average of 4.2 eggs per inch.

The general average from the counts made so far is about 4 eggs per inch of gallery.

Total Length of Egg Gallery

Keen (*U130*) states: "The maximum length of a gallery which any pair of beetles would form was not determined, but it was found from averages that beetles constructed at least 17 inches of gallery per attack and 187.8 inches of gallery per square foot of bark."

Measurements reported by Patterson (*U218*) from the Jenny Creek area of Oregon showed averages ranging from 8.4 to 14.5 inches of gallery per attack. These measurements apparently were made while the extension of galleries was still in progress and before the beetles had completed the full length of excavation.

From a measurement of egg galleries on 4 square feet of infested bark, Person (*U238*) reported an average of 131 inches of egg gallery per square foot of bark, or 10.9 inches of gallery per attack.

In a study of beetle behavior in high and low risk trees Yuill (*U346*) in 1941 found an average of 156 inches of gallery constructed per square foot in samples from 80 trees. There was no difference between the high- and low-risk trees.

A summary of all data taken on egg gallery length shows a general average of about 14.0 inches constructed for each attack and about 162 inches per square foot. This figure, of course, is subject to wide variation depending on the density of attack and the success of brood development.

Ventilation Holes

Hopkins (*44*) states:

> Ventilating burrows are the vertical (sic) burrows located at frequent intervals in the roof of the egg gallery and extending outward to or near the surface. They are utilized by the parent adults as a place in which to turn around, or in which to pack the boring dust, or through which to eject the dust, as the case may be.

Subsequent observations and studies have confirmed Hopkins' statement as to the purpose of ventilating burrows in most respects. But it remained for Buckhorn (*U38*) to show that the real purpose of the open holes was not to ventilate the egg galleries or to discharge boring dust but to provide an exit for emerging parent adults. He states:

> This finding was verified by careful observation throughout the season (1934). After construction of the gallery is under way, holes of various depths are bored by the parent adults into the outer bark. Many of these extend to but do not attain the outer bark surface. No openings are made through the surface until a parent adult emerges and leaves an open exit hole. No adult forms of secondary insects were noted to enter the *D. brevicomis* galleries until a parent adult had emerged and left an open hole as a means for their entrance. Prior to emerging the parent adults feed around in the inner bark. This feeding character can easily be recognized as a short section of the gallery is usually enlarged, forming a large chamber from which several short galleries may extend. These feeding places are always free from frass and are found at the base of the exit hole.

The number of ventilating holes per attack and per square foot of bark has been given attention in bark counts largely for the purpose of separating them from the count of new adult exit holes. In the "toothpick method" of making bark counts they have been separated from exit holes whenever a toothpick completely penetrated the bark from an egg gallery (*U182*).

Bark counts on the Ashland, Oreg., area reported by Keen (*U130*) showed an average of 9 vent holes per square foot in an examination of 40.8 square feet of bark; and from an examination of 200 attacks, an average of 2.1 vent holes per attack. From an examination of 330 square feet of bark in the Rogue River (Oregon)

area, Glendenning (*U72*) showed an average of 16.4 vent holes per square foot. In summarizing the bark counts made on the Rogue River area between 1914 and 1923, Patterson (*U218*) shows an average of 21 vent holes per square foot from an examination of 1,857 square feet of bark. This number of vent holes is roughly in proportion to the number of parent adults found emerging per square foot of bark.

Re-Emergence of Parent Adults

Soon after gallery construction has commenced, some parent adults may bore out through the bark and seek more favorable opportunities elsewhere (*U38*). However, as Buckhorn has shown, the majority remain under the bark and do not emerge at all or emerge 15 to 18 days before the new adults start emerging.

This habit of re-emergence was not noted by Webb (*144*) who reported that the parent adults remain in the galleries until they die. Re-emergence, however, has been found in practically all subsequent studies dealing with the habits of the parent adult beetles.

Re-emergence was first reported by Keen (*U130*), who caged a down log containing an overwintering brood composed of parent adults and eggs. A green log was also placed in the cage to attract any parent adult beetles that might emerge. These did emerge during March, April, and May, and reattacked the down log. It was also noted in the field that parent adults were emerging before new adults had formed, and that their attacks were largely confined to the base and uninfested parts of previously attacked trees. From a count of 20 square feet of bark, it was determined that about 57.5 percent of the parent adults had emerged, and that this emergence had occurred "about the time the brood reached the three-quarter grown larval stage."

Furniss (*U68*) investigated the activities of re-emerged parent adults on the Modoc National Forest of California in 1933 by caging and forcing attacks on standing trees during the summer. He found that:

1. Parent adult beetles emerged to the extent of 53.6 percent of the attacking population.
2. Parent adult emergence began when the progeny was about a quarter-grown, reached its peak when the larvae were half-grown and ceased just prior to the time that new adults emerged.
3. Re-emerged parent adults were capable of establishing a second brood which developed to maturity.

Salman (*U270*), assisted by Bongberg, made a thorough study of the activity of re-emerged parent adult beetles on Modoc National Forest in 1934. Cages were constructed on newly attacked trees to trap the emerging parent adults from each seasonal generation; these re-emerged adults were then forced to attack caged trees, and the success of their attack was determined. It was found that:

1. This season's work showed re-emergence to be a normal habit. Re-emergence followed the attacks resulting in the 3 primary generations of the 1934 season.

2. In the first generation emergence of parent adults from 20 caged trees ranged from 2.1 to 36.9 beetles per square foot and averaged 19.1. It was estimated that the re-emerged population had a force about one-twelfth (8.2 percent) as great as that of the adults emerging from overwintering trees.

3. In the second generation, re-emergence from 6 cages ranged from 4.8 to 42.0 beetles per square foot. It was estimated this re-emergence had had an effectiveness nearly one fifth (19 percent) as great per unit of bark surface as the progeny of the first generation.

4. In the third generation, which attacked in the fall, some re-emergence of parent adults occurred before cold weather set in, but it was considered that many of them which overwintered in the trees re-emerged the following spring.

5. The sex ratio of re-emerged parent adults was variable, but averaged 40.2 percent males and 58.8 percent females.

6. Pure attacks of re-emerged parent adults resulted in normal development and progeny in normal amounts.

7. A second re-emergence of parent adults was found to occur late in the season. These beetles had emerged for the first time as progeny from overwintering trees, attacked a standing tree from which they re-emerged, and attacked a second standing tree from which they made their third emergence. These beetles were very few in number.

8. Beetles which had made the second re-emergence attacked a caged log and produced a brood from which some small sized adults developed. Abnormal brood development was attributed to poor conditions in the trap log.

The Egg Stage

The generic character of the eggs of the western pine beetle is described briefly by Hopkins (*43*). "The eggs . . . have not been studied in detail, but they are short, oval to oblong-oval, pearly white and shining, and apparently without distinctive generic or specific characters." No more specific description of the egg of this species has been found anywhere in published literature or manuscripts.

Number of Eggs Per Female

In the early work at Ashland, Oreg., Keen (*U130*) states: "The maximum number of eggs laid by any one female was determined as 41 with an average of 30." But . . . "this figure is undoubtedly too low, as it is difficult to get the complete egg laying capacity of a female without disturbing or injuring her in some way." By counting the number of eggs in a sample length of gallery and determining the inches of gallery per square foot, and the number of attacking females per square foot, Keen estimated 64.5 eggs per female and 93.6 eggs per attack. Reporting on 55 galleries counted by Sergent, Patterson (*U218*) gives the average number of eggs per gallery as 35.4.

On the basis of the general average of 4 eggs per inch of gallery and 14 inches of gallery per attack, the average number of eggs per

attack should be about 56, and the average number of eggs per female 48. Like many other statistics, these are subject to wide variation owing to differences in numbers of attack per square foot of bark, inches of gallery constructed, and egg laying capacity of different individuals. They can only be considered as indicative.

Period of Oviposition

"Commencing with the first eggs which are usually laid about 8 days after attack, egg laying continues from 10 to 49 days with an average of about 23 days. This egg-laying period, of course, is extended in the case of females which overwinter before depositing their full complement of eggs" (*U130*).

Incubation Period

Webb (*144*), referring to first generation trees at Centerville, Idaho, states: "These eggs hatch in about 4 days after deposition." Chamberlin (*17*) states that "the eggs hatch in a week or 10 days." Struble (*U295*), transferring individual eggs from the bark in a series of experiments, noted that "the eggs in practically every instance hatched 1 to 5 days after transferring to petri dishes." Jeffrey (*U108*) states: "These eggs hatch in somewhat over a week." Person (*U238*) recorded 7 days from first egg to first larva for the first seasonal generation, 8 days for the second generation.

Beal (*U6*) made a laboratory study of the effect of temperature upon incubation in 1931. A series of 250 recently laid eggs were isolated in lots of 50 each on moist blotting paper in covered petri dishes and exposed to constantly maintained temperatures with the following results:

At 60° F.—20 out of 50 eggs hatched in 16 days.
At 55° F.—14 out of 50 eggs hatched in 16 days.
At 53° F.— 7 out of 50 eggs hatched in 16 days.
At 40° F.— 0 out of 50 eggs hatched in 21 days.
At 36° F.— 0 out of 50 eggs hatched in 21 days.

This test was conducted to determine the lowest temperature at which eggs would incubate. The results indicate the minimum temperature to be around 50° F. Beal states that "eggs hatched at approximately the same temperatures at which larval and pupal development began."

It is obvious from all of these observations that the rate of incubation of western pine beetle eggs is regulated by temperature; that development begins just above 50° F. and is very slow up to 60°. Optimum temperatures under which incubation is completed in 7 days are probably between 70° and 90°.

The Larval Stage

The technical description of larval characters given by Hopkins (*43*) is too long to be quoted here. In general appearance, the larvae of the beetle are small, white, subcylindrical, wrinkled, curved, legless grubs about one-fourth inch long with a small yellow head. They may be found by slicing through the bark of an infested ponderosa pine.

The Larval Mine

The larval mine has been described by Keen (*U130*):

> The larva upon hatching commences boring its gallery at right angles to the egg gallery. The first one-eighth of an inch is usually under a small layer of the bark, then it goes deeper so that the bark is cut and the cambium reached, and sometimes the sapwood is faintly scored. After about half an inch or more of gallery, it returns to the bark or inner bark and commences working outward towards the outer bark. After about 7 days, it reaches the junction of the inner and outer bark where most of its development occurs. After it has nearly completed its growth, it bores further out into the bark and forms an enlargement of its gallery in which to pupate.

The mine is at first very tiny, being just large enough to accommodate newly hatched larva (fig. 6); it steadily increases its size with the growth of the larva and is tightly packed with sawdust except for the outer end where the larva is feeding.

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FIGURE 6.—Typical winding egg galleries of the western pine beetle on the inner surface of ponderosa pine bark, showing the start of larval mines.

Food Habits of the Larva

The larva must obtain its food from the cambium, phloem, and outer bark because it does not develop in other parts of the tree. These three areas contain several organic substances, but just which ones are utilized in nutrition is a question that has not been definitely answered. Jeffrey (*U108*) suggests that the cambium area supplies the most available larval food material because "in this part of the tree, tree growth is taking place and the supply of larval food material, especially proteins and simple sugars, would probably be greater than in the wood or outer bark."

Interest in the nutritional requirements of the larva was stimulated in 1929 and 1930 by the theory that here would be found the explanation for the selection of certain trees by the beetles. Preferred trees were thought to have a higher content of nutritional material than trees that escaped attack. Struble (*U295*) tried to determine what food elements are essential to development of the larvae by isolating individuals in artificial media and feeding them. It was planned to test certain organic substances that were known to be important in the nutrition of other insects. These experiments were abandoned after a number of rearing media failed and it was found that the natural inner bark of the tree affords the only conditions in which the larva can be carried through its earlier stages of development.

Jeffrey (*U108*) began an analysis of organic materials found in bark tissues in which the larvae feed. He pointed out that when the larvae are about one-quarter grown, they make a very abrupt and radical change in their environment and in the media in which they feed. "They move from the living bark (inner) which is comparatively soft and has a high moisture content (60 to 70 percent on the fresh basis) into the outer dead bark, which is very hard but non-fibrous and contains only 6 to 9 percent moisture."

When the larvae bore into the outer bark, they have by no means exhausted all of the inner bark tissue; so food supply does not explain the reason for this movement. Jeffrey did find an explanation, however, in the chemical changes that take place in the inner bark following an attack:

> The natural medium in which *D. brevicomis* passes the critical parts of its life history is enormously more complex than that of either the termite or *Drosophila*. When the insect enters the tissue, the latter is alive. A mechanical injury, or girdling, is produced and micro-organisms of at least 2 kinds—yeasts and 'bluestains' (*Ceratostomella* sp.)—are introduced. The girdling alone would be enough to cause a considerable change in the condition of the tree, but with the addition of the micro-organisms the change is enormous. In one log investigated the total sugar concentration rose to twice the initial value, and subsequently dropped to one-twentieth of the highest value recorded. There was also a continuous change in the ratio of different sugars. The writer finds that by the time the larvae leave the inner bark the sugar concentrations there have fallen lower than in the outer bark to which they migrate.

These results of Jeffrey's work not only help to explain why the larvae migrate into the outer bark, but they also indicate that one important source of nutrition may be the unreduced sugars of the cambium, phloem, and outer bark.

Micro-Organisms Associated With the Larvae

Jeffrey's work also served to emphasize the importance of certain micro-organisms during the feeding period of the larvae, particularly a yeast first brought to notice by Struble (*U295*) and Person (*112*). According to Person, this yeast was "always present on the larvae and new adults of the beetle." At first the yeast was thought to be a *Torula*, but later was determined as *Saccharomyces pini* (Holst.). It produces fermentations in the inner bark very soon after the entrance of the parent adult beetle, and the young larvae begin their feeding in tissues where active fermentations of sugars are in progress. In fact, no development of larvae has been observed except in association with this yeast. Whether this is a true symbiotic relationship in which the action of the yeast on the plant tissues is necessary to make the material available as food for the insect was not determined.

The Larval Instars

As the larva grows, it goes through periodic molts or instars during which it sheds both the soft larval skin and the hard chitinized head capsule. With each molt the body gains appreciably in size, and the new head capsule that is formed is definitely wider. It has been practically impossible to observe these changes, because the larva throughout its development is concealed in its feeding galleries. The cast skins are soon lost in the frass or eaten by other insects that inhabit the galleries.

It was not until 1934 that an attempt was made to determine the number of larval instars of the western pine beetle. The first work was undertaken by Salman (*U268*), who determined that the larvae pass through four instars. Further detailed work was reported by Salman and Bongberg (*U282*), who approached the problem by measuring the changes in head-capsule widths during the development of broods in infested trees. By collecting infested bark at 2-day intervals, killing the larvae by boiling, and later measuring the head capsule, they found that four distinct changes occurred. They concluded that:

1. The western pine beetle passes through 4 instars in its larval development.
2. There is no indication of extra instars occurring in the development of some individuals or of one sex.
3. The larvae of the first instar are to be found in the phloem.
4. The larvae of the second instar occur in both the phloem and outer bark. Apparently the migration from phloem to bark takes place in this instar.
5. The larvae of the third and fourth instars are to be found in the outer bark.

Period of Larval Development

When western pine beetle larvae have a food supply, they continue to feed and grow as long as there are temperatures under which they can maintain normal metabolism. Favorable moisture conditions must also be maintained, although changes in them do not seem to affect larval development as immediately or as drastically as temperature changes. Most of the studies dealing with moisture and temperature requirements have been concerned with the larval stage.

The first observations on larval development revealed that: Growth under natural field conditions slowed down as cold weather came on in the fall; the larvae remained practically dormant during the winter period; and the normal rate of development was resumed as warm weather returned in the spring. Also when infested outer bark was collected during the dormant winter period and brought into a warm room, the larvae soon started developing and continued on to the stages of pupae, new adults, and emergence if the bark was kept warm.

Webb (*143*) first recorded the length of time spent by first-generation larvae in trees near Centerville, Idaho:

> It would appear that the length of time spent in the larval state is from 31 to 35 days. Sometimes, however, a few individuals of this first generation, either from retarded development or other causes, do not go through their transformations with the rest of the broods, but remain as larvae all through the fall and winter, evidently changing to pupae the following spring. . . . Thus it may require from 300 to 390 days or more for the complete development and emergence of some individuals of the first generation.

Keen (*U130*) obtained records of the larval development period under natural field conditions near Ashland, Oreg., in 1915 and 1916. He made repeated examinations of broods in a series of 23 standing, infested trees; by averaging the time from hatching of the eggs to formulation of the pupae, he concluded that "these records show the larval development period to be about 30 days for the first seasonal generation, 60 days for the second generation, and 155 days for the overwintering generation."

Records of infested trees kept by Miller (*U181*) in the southern Sierra Nevada in 1918, and some kept by Patterson (*U214*) in the Yosemite National Park in 1919, show nearly the same rates for larval development as those recorded by Keen.

From a series of 10 infested trees on an area near North Fork, Calif., for which intensive records of brood development were kept in 1926, Person (*U238*) determined that the period from "first larva hatching" to "first pupa formed" averaged 20 days for both the first and second seasonal generations. Person's records refer to the average period during which the larvae of each generation were found in the trees and not to the development of individual broods.

In following the development of larvae in infested trees in the same area, Furniss (*U68*) found considerable difference in the period of larval development between generations and between seasons. His data can be summarized as follows:

Season:	Period of larval development 1932 (days)	1933 (days)
First seasonal generation	45	75
Second seasonal generation	34	75
Overwintering generation	165	—

The difference between the two seasons was attributed to climatic variation:

> The only apparent difference was in the cold period which followed the early warm temperatures. In 1932 the cold weather was sufficiently delayed for the first seasonal generation to become fully established. In 1933 the cold weather stopped the emergence of the overwintering generation before it had fairly begun and emergence did not begin again until a month later.

Temperature and Moisture Requirements

In the field studies reported by Person (*U238*), no attempt was made to determine the actual range of temperatures under which the larvae were active, nor the low and high temperatures that limited their development. It was generally accepted that the temperature responses of the western pine beetle were similar to those of many other insects that become active at temperatures around 50° F. and reach their maximum activity under temperatures between 70° and 90°. Little was learned concerning moisture requirements.

It was not until 1929 that an attempt was made to determine with some degree of accuracy the temperature and moisture conditions most favorable to the beetle. Beal (*U6*) began a series of field studies in slash in southern Oregon and measured the temperatures and moisture conditions under which brood development took place. Beal's work between 1929 and 1931 was limited to such variations of temperature and moisture as were found in the field; he made no attempt to regulate these factors.

In 1931 Beal moved these studies into the laboratory at the University of California, where temperatures could be controlled. Here the rate of brood development was followed in infested logs and bark sections placed in insulated compartments; air temperatures were held within plus or minus 2° of these figures: 35°, 40°, 48°, 52°, 60°, 65°, 70°, 75°, 85°, 95°, 100°, and 106° F. Atmospheric humidity was regulated by ventilation but was not controlled. Moisture content of the bark and phloem was determined at intervals during the progress of the experiments. The following material was used in the studies:

1. Log sections in which a successful attack had been established with the parent adults and egg stages predominating. These were placed under each of the maintained temperatures. Development of the broods was then checked at frequent intervals, and moisture percent of the phloem and inner bark less frequently. The moisture percent was found to be high at all times, averaging from 200 to 300 percent in all logs except those kept at the highest temperatures. Material kept at higher temperatures had a slight tendency to dry out. Brood development in most of the tests could be followed only part way through the larval stage because of high mortality that set in after a few weeks.

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2. Selected mature larvae not yet in the prepupal stage, obtained by shaving infested bark. These were placed in outer-bark sawdust and subjected to the same range of temperatures and moisture conditions as the log sections. Mortality of these mature larvae was low, and their development could be followed through the prepupal, pupal, and new adult stages.

3. Selected mature larvae as in 2 above. These were subjected to temperatures alternating between 40° and 75° F. for varying periods. Their development was followed to determine whether fluctuating temperatures corresponding to those in the field would result in responses differing from those obtained at constantly maintained temperatures.

The results of field and laboratory studies were summarized as follows (*U6*):

1. Brood development of this insect begins at about 50° F.
2. The rate of development increases directly with the temperature up to about 80° F.
3. Constant temperatures of 95° F. and above if sufficiently long maintained are fatal to all stages (of larvae).
4. Most rapid development occurs at about 85° F., but the most successful development from the standpoint of greatest numbers of insects produced is in the vicinity of 70–75° F.
5. Phloem moisture of infested felled material increases or remains abnormally high in all cases except at high lethal temperatures where some drying occurs.
6. Failure of broods to develop at low temperatures below 50° F. and at high temperatures above 95° F. is probably due to the effect of limiting temperatures.
7. Brood failure occurring within favorable temperature zones are probably due to excessive moisture of the inner bark or some factor closely associated with it.
8. Daily changes in temperature appear to have no stimulating effect upon brook development.
9. A definite number of hour-degrees of effective temperature is necessary for the development of a specific brood stage of the western pine beetle.

In these studies Beal was unable to establish the total number of effective hour-degrees required to carry the larvae through from egg to prepupal stages. However, the results furnished convincing evidence that the rate of development is dependent on accumulated hour-degree temperature above 50° F. "The hour-degrees obtained by the summation of alternating temperatures and the summation of different constant temperatures in both experiments gave about 10,000 hour-degrees for development of mature larvae to final adults."

Beginning in 1934, Salman (*U270*) undertook a series of studies to determine whether the relationships between temperature and brood development already indicated by the laboratory studies of Beal and others could be confirmed by records in the field. His objectives were to determine "the relationship of air temperatures to bark temperatures, and the temperature requirements of broods developing normally in the bark of infested trees." It was thought that a record of air temperatures from ordinary weather stations could be used as an index to important seasonal activities of the beetle,

and that seasonal events critical in the timing of control work, such as the spring emergence, could be forecast with some certainty from weather records in the infested areas.

Temperature and brood development were recorded in two localities with significant climatic differences—near North Fork, representing low elevation, west slope conditions in central California; at Hackamore, representing the high plateau conditions in northeastern California. Bark temperatures were measured by specially designed thermographs which gave a continuous record within the bark at the depth where larval development took place. These records were maintained in a series of trees at a height of 10 feet or more above the ground. Another set of temperature readings was obtained from two trees by means of a potentiometer and thermocouples which compared air and bark temperatures at varying heights up to 80 feet above the ground. Brood development was observed by frequent examinations of infested bark, and ultimate emergence was recorded by screening bark areas on standing infested trees to trap the adults as they emerged. All together, about 50 infested trees were included in these studies.

In discussing the relation of bark to air temperatures under the range that occurs during the season of beetle activity, Salman (*U270*) made the following summary:

> Perusal of bark temperature records shows that each tree has a characteristic curve. The characteristics of each curve have been found to be dependent, in part at least, on the hours during which sun strikes the bark surface.
>
> On basic records from 6 trees there appears to be little possibility of correlating air and bark temperatures in small units such as hours or even days. However, weekly summations do show a distinct relationship. There are indications of a fairly constant response of bark temperatures to air in the mid range, a resistance to absorption of heat at higher temperatures, and a decided resistance to loss of heat at the lower ranges.
>
> One point of importance brought out is that bark temperatures (accumulated) during a given day are higher than air temperatures. A temperature surplus is accumulated each day. On some trees this surplus is great, on others slight.

As to the relationship of brood development to air and bark temperatures, Salman considered the results of the tests unsatisfactory because of inadequate records of brood development. He was able to tabulate the hour-degrees required from first larvae to first pupae from only one tree. This shows a total of 7,127 hour-degrees for the entire period of larval development. Apparently because of the many variables encountered in these studies, no attempt has been made to use weather records in the field as a basis for estimating the condition of brood development.

Yuill (*U341*) attempted to relate air and bark temperatures at the base of a tree to bark temperatures at different heights on its main bole. Bark temperatures were measured by means of thermocouples inserted at the depth of developing brood stages. Comparative air temperatures were also read by thermocouples. Because of difficulties in developing a type of thermocouple adaptable to the

bark, many important readings were considered unreliable. Yuill, however, considered the following points established:

a. Air temperature is the same at different heights along the trunk, except for a slight effect of radiation at the base.

b. Probably due to radiation, the bark temperatures at the base of the tree reach slightly higher and lower extremes than those higher on the bole.

c. Bark temperatures in areas exposed to the sun tend to rise above air temperature, and when shaded tend to revert to air temperature. There is considerable lag in these changes, so that the bark temperatures do not reach the lower extremes that air temperatures do.

d. The warmest side of the tree lies between the west and south exposures.

e. Where shade is not a modifying factor, bark temperatures recorded by a bulb-type thermograph at a given point are representative of the bark temperatures at other points on the same side of the tree.

Larval Population

Glendenning (*U72*) in 1919 counted larval populations at Ashland, Oreg., by shaving 330 square feet of bark samples from a series of 67 infested trees containing overwintering broods of western pine beetle. Three or more samples of 1½ square feet each were taken from 4 to 20 feet above ground on at least 3 sides of trees. These counts showed 185 larvae per square foot of bark in the advanced larval period from January 1 to April 1, and 122 per square foot in the prepupal period from April 1 to May 24.

Another count of larval population was made after the cold winter of 1932–33, when 1,143 bark samples were collected by forest rangers from 33 localities in eastern Oregon and Washington during the period January 1 to April 6, 1933, and sent in to the Portland Forest Insect Laboratory. The live and dead larvae were carefully counted to determine the effect of the freeze. An average of 189 dead and live larvae were found per square foot of bark in the 782 square feet examined.

The Prepupal Stage

As the larva approaches the end of its feeding period, it makes an elongated cell, just large enough to accommodate the full-grown stage, at the end of its mine in the outer bark. This cell is kept clear of borings, and here the larva goes through a resting period before it is ready to pupate. According to Salman and Bongberg (*U283*): "Just preceding pupation, fourth instar larvae enter a physiological condition that is known as the prepupal stage." As the larva passes into this prepupal condition, great changes take place in its body functions. Feeding ceases and is not resumed until the adult stage is reached. The body becomes soft and shows little reaction to stimuli. Internal changes take place preparatory to the regrouping of the body cells to form the entirely new characters of the pupae and adult.

Descriptions of the prepupal stage are lacking in published literature and in manuscript reports. Externally, the prepupal larva still resembles the fourth instar, but it can easily be distinguished

from mature larva by certain characteristics of appearance and posture. The prepupal larva becomes sluggish and lies in a distended relaxed position, with head generally pointing toward the center of the tree, whereas mature larva is active and curls up its body when disturbed. In color the prepupal larva is yellowish white, whereas mature larva is white or slightly pinkish white. The prepupal larva is entirely opaque; in mature larva, ingested material in the alimentary canal can be seen in shadowy outline through the external skin. The thoracic segments of the prepupal larva tend to enlarge and show some differentiation from the abdominal segments.

Since the prepupal stage is an inactive one during which the larva does not feed or move about, no particular events are connected with development until the pupa takes form. However, internal changes that take place preparatory to pupation cannot go on unless the larva is subjected to adequate temperature within its developmental range. The temperature required for the development of prepupal larva present an important departure from that required for the development of younger larva.

Investigators who have followed the development of western pine beetle broods in the field have been puzzled by the absence of pupae during the winter period. Where broods in the fall develop up to the mature larval stage, they rest at that point although broods still in the younger larval stages continue to develop. Furniss (*U68*) commented:

> The fact that most of the third generation passes part of September and all of October and November in the large larval stage while other stages were in the process of development is outstanding. Apparently prepupal larvae have a considerably higher temperature requirement for transformation than do the other stages of this insect.

Whiteside (*U331*) made a thorough laboratory study in 1934 of the temperature requirements for the development of prepupal larvae. He subjected mature larvae, which he had removed from bark, to constant temperatures under a controlled relative humidity of 55 to 66 percent. Constant temperatures ranging from 32° to 74° F. were included in the experiment. The results indicated special temperature requirements for the change from mature to prepupal larva.

> In the fall of the year, the physiological change from the last active fourth instar larval stage to the prepupal conditions acts as a bar or a barrier and prohibits the transformation to the pupal stage at a temperature near the zero of development (about 50° F.).
>
> For mature larvae removed during the early fall, the zero of development lies above 50° and closer to 55° F. Once the prepupal condition has actually been attained, the metamorphosis to the pupal and thence to the callow adult stage will continue uninterrupted at temperatures as low as 45° F. Indications are that this phenomenon will take place at temperatures as low as 41° F.
>
> For mature larvae removed during the early spring (February and March), the zero of development appears to be below 50° F.,

probably closer to 45°. A certain amount of feeding and development during the winter enables the larvae to transform rapidly to pupae and thence to callow adults with the rise of temperatures in the spring.

Whiteside's report (*U331*) showed considerable variation in the time required for transformation from larvae to pupae, depending upon whether the larvae subjected to constant temperatures were removed from the bark in the fall or in the spring. However, the time is probably best represented by a test in November with larvae from an overwintering brood:

°F:	*Average time from prepupal larvae to pupae (days)*
74	2
65	3
60	4
55	7

When mature larvae were exposed at 50° F., a few pupae formed after 117 days. This indicated that some development took place at 50°. After the prepupal stage was reached, they transformed to pupae in about 18 days.

The greatest significance of the prepupal stage seems to lie in the temperature requirements that prohibit or retard development under field conditions at the beginning of winter. As a rule, larvae that complete feeding in the fall go into the prepupal stage, continue into the pupal and new adult stages, and, if a few warm days occur, emerge before winter temperatures set in. Mature larvae that do not develop to the prepupal stage rest in the outer bark until warmer temperatures arrive in the spring. In the meantime, younger larvae continue to develop during the warmer days of the late fall and winter until they reach the temperature bar for transformation to prepupae. Consequently, when warmer weather arrives in the spring, practically all broods are in the mature larval stage and ready to develop to prepupae.

The Pupal Stage

The transformation from prepupal larva to pupa takes place quickly without feeding or activity other than the internal and external changes that go on in the body of the insect. Hopkins (*43*) gives a technical description of the pupa. Very close to the mature beetle in size, the pupa is white or creamy white in color; most of the appendages and external characters of the adult are present as pad-like masses of tissue; the abdomen extends well out beyond the wing pads and is characterized by noticeable soft spines; the entire body is soft and delicate and is incapable of movement except for spasmodic, rotationlike movements of the abdomen when disturbed.

The insect does not remain long in the pupal stage unless long periods of low temperatures occur. In the first seasonal generation Webb (*144*) found that "the length of time spent in the pupal stage is approximately 15 days." Keen (*U130*) followed the development of pupae in infested trees near Oshland, Oreg., and concluded:

> . . . an average duration period from larva to adult of 18 days for the first seasonal generation, with a minimum of 6 and a maximum of 38 days. For the second generation this duration

period averaged 40.7 days, with a minimum of 13 days and a maximum of 92 days.

Miller (*U181*) and Patterson (*U214*) reported that the length of time during which pupae were present in individual trees ranged from 7 to 20 days. Person (*U238*) in 1926 recorded 8 days for the first seasonal generation, and 6 days for the second generation.

Whiteside (*U331*) was able to follow a number of individual pupae through their transformation to new adults, and he found that their development varied with the constant temperatures to which they were exposed:

°F:	*Average time from pupa to callow adult (days)*
74	6
65	6
60	12
55	24
50	51

This record confirms previous observations that under favorable conditions the minimum time in which pupae can complete their development is about 6 days.

In summarizing individual tree records, Salman and Bongberg (*U283*) state:

> There are 18 records available concerning the time required for completion of development under field conditions. These indicate from 6 to 38 days are required. In May, from 10 to 29 days were required. In late July, August, and early September from 6 to 18 days were spent in the pupal stage.

The Callow Adult Stage

The term "callow adult" is used to designate the stage that immediately follows the pupa. At this time the appendages and organs of the adult have taken form, and free movement of the beetle becomes possible. The callow adult differs from the mature beetle mainly in the nature and color of the external shell. Its shell is not fully sclerotized and is still soft; it is yellowish in color at first and gradually changes to brownish yellow as hardening of the chitin advances. The shell of the beetle when finally mature is dark brown to black.

The change from callow adult to mature beetle takes place gradually. The beetle remains in its pupal cell while the hardening and coloring process is going on, and does not start to bore outward until nearly mature. Available reports contain no record of studies to determine the time that the beetle spends in the soft-shelled immature condition of the callow adult. It has apparently been considered a relatively unimportant phase of the insect's development.

The Pre-Emergence Period

Well (*144*) noted that the new beetles, even when they have become fully sclerotized and apparently mature, rest for a period before they leave the infested tree.

When first transformed, in May and June, the young beetles have very soft, delicate tissues. They therefore remain in their pupa cases until their bodies are fully hardened or chitinized.

> When nearly ready to emerge, the adults bore their way almost to the surface of the bark, but pause before emerging, appearing to rest in the burrows they have just made. . . . The length of time spent in the bark after reaching this stage (adult) appears to be from 7 to 14 days.

The period spent by the adult beetle in the outer bark before it emerges was also recorded in the Ashland studies in 1916 (*U130*):

> The adult event period or the time between the maturing of a beetle and its emergence averages 18.2 days for the overwintering generation and 7.1 days for the first generation. The duration and event periods are prolonged in the spring and accelerated in the fall.

Subsequent studies have not given attention to this phase of the adult's existence.

Emergence

The act of emergence when the beetle comes through the last scales of the outer bark was first described by Webb (*144*):

> When quite ready to emerge, the beetles continue their burrows out through the remaining portion of the bark. The individuals of a brood do not appear to emerge simultaneously, but they come forth at irregular intervals until all are out, leaving the bark thickly punctured with small, round, clean-cut holes.

Period of Emergence and Influence of Temperature

Keen (*U130*) states: "The emergence of beetles from a tree extends over a considerable period of time and is not concerted. A few hot days will cause the beetles to leave the tree in swarms, while a week of cold weather will almost completely stop emergence." He records the average period between the first and last emergence (from the same tree) to be 38.5 days; straggling emergence from one tree extended this period to 99 days. Hopping (*51*) reports a few beetles of the genus *Dendroctonus* holding over in abandoned trees and not emerging until the following year.

Temperature conditions undoubtedly account for a lag in emergence of overwintering broods from the north side of a tree as compared with the south side. The north side is shaded while the bark on the south side may be warmed by the sun. Evenden (*U59*) records an average difference of 12.2 days in the final emergence between the north and south sides from a series of 12 trees near Coeur d'Alene, Idaho. In summarizing the records of Keen and others, Miller (*U177*) states:

> Overwintering broods in the south side of a tree may emerge from 27 to 41 days earlier than on the north side of the same tree; the average is 35 days earlier. Broods in trees of the first seasonal generation which emerge during the summer months and do not overwinter appear to develop at about the same rate on all sides of the tree.

Furniss (*U64*) noted this lag in emergence on the north side of trees near North Fork, Calif., as ranging from 21 to 68 days.

Buckhorn (*U37*), who used cages to trap beetles emerging from infested trees on Ochoco National Forest in central Oregon, reported: "Since the emergence records were taken at about 7-day intervals,

is was not possible to determine any small variations due to exposure on the tree. The emergence started and ended on approximately the same collection dates, but the peak of emergence from the south side of trees occurred about 8 days earlier than on the north side."

Although it has been definitely determined that emergence of adults of a generation of beetles may extend over a fairly prolonged period, the great bulk of the population emerges in well defined peaks lasting only for a few days or a week. These peaks of emergence usually coincide with the first days of warm weather after the pre-emergence period, and they may be abruptly interrupted by a spell of cold weather. Salman (*U270*), who followed emergence in the Modoc areas in 1934, found that "emergence of the main group of second generation trees (overwintering) occurred in 2 peaks, one during the middle of May and the other during the middle of June."

The emergence records obtained by maintaining traps on both overwintering and summer brood trees during 1933, 1934, and 1935 on Modoc National Forest of California were summarized by Salman and Bongberg (*U283*). Emergence per square foot of bark was related to daily air temperatures (fig. 7). Two definite peaks of

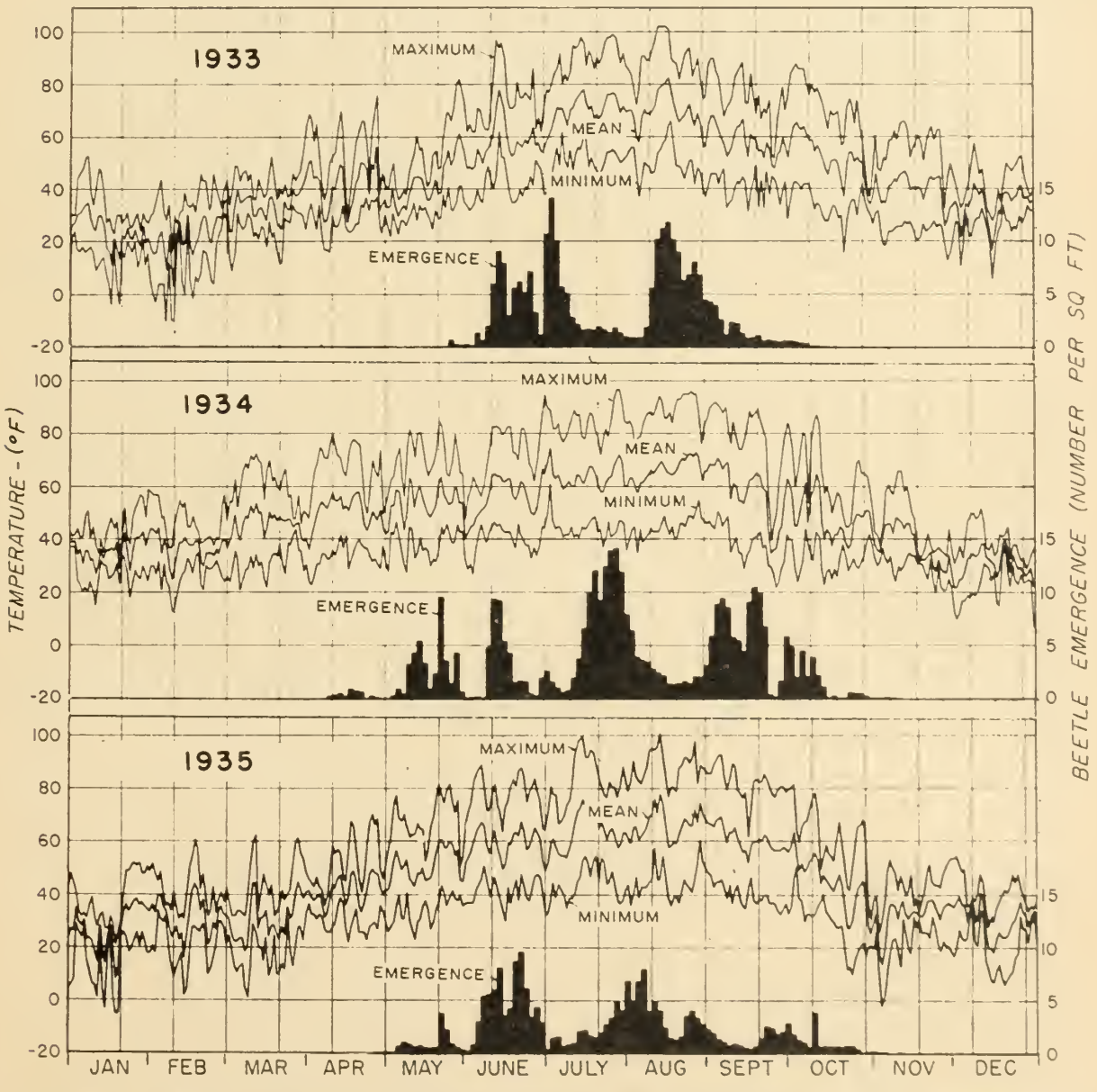

FIGURE 7.—Western pine beetle emergence in relation to air temperatures. Modoc National Forest, Calif., 1933–35.

emergence occurred from the overwintering trees each season, but at different periods. The season of 1934 was about a month earlier than 1933 or 1935 in the emergence from both winter and summer trees. The season of 1935 was marked by late emergence extending well into November. The authors reached the following conclusion: "Emergence starts as a result of temperatures that are frequently 60° F. and above; emergence generally ceases soon after maximum temperatures are frequently below 60° F. These statements are but rough rules of thumb based on 3 years of records."

Exit Holes

The clear-cut beetle exit hole that the insect leaves in the bark surface as it emerges has received considerable attention from investigators interested in population estimates. Since most new adults bore directly out from their individual pupal cells in the outer bark, the number of exit holes per unit of bark surface has been taken to represent the number of adults emerging from it. As a result, the exit holes have been counted in hundreds of bark samples to arrive at estimates of the numbers of beetles which took flight in certain areas. Ventilation holes have been separated from exit holes in these statistics. In summarizing these counts up to 1928, Keen (*U142*) emphasized the great variability in the number of exit holes per square foot of bark surface: from 0 to 340 per square foot, around a mean of 63.

Salman, referring to studies in 1934 in northern California (*U270*) states: "Recent work has shown counts (of exit holes) give results considerably lower than actual emergence."

Buckhorn (*U38*) compared the averages for trapped emergence of beetles with number of exit holes in the same bark surface and reported:

> The least number of beetles per hole was .4 and the highest 3.0, while 1.3 and 1.4 beetles per hole emerged most frequently. The 6 cases in which less than 1 beetle emerged are unaccounted for. This may be a natural phenomenon or due to beetles escaping from cages or getting lost or destroyed before collection.

The average emergence was 1.46 beetles per exit hole.

It is obvious that exit hole counts cannot be used to indicate the exact number of emerging beetles (fig. 8), but they can serve as a satisfactory index to emerging beetle populations. Consequently, the ratio of attacks to exit holes has been generally used in population studies as an indication of brood success.

THE TOTAL BROOD PERIOD

Time Required for Development From Egg to Adult Emergence

Full brood development from egg to adult emergence requires a widely variable period. The time is dependent largely upon the seasonal generation involved and the climatic conditions of the locality, and differences in the time for total brood period reflect the temperatures to which the broods are exposed during development.

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FIGURE 8.—Bark showing exit holes of western pine beetle and a larger hole drilled by a woodpecker in search of bark-boring larvae.

At Centerville, Idaho, Webb (*144*) records one tree in which "eggs were deposited July 6 and the broods developed and emerged by August 28, a period of 53 days." However, overwintering broods ". . . may require 300 to 390 days or more for the complete development and emergence of some individuals."

For southern Oregon, Keen (*U130*) determined that the average brood period from first egg to first adult emerging for the first seasonal generation was 63 days; for the second or overwintering generation, 279 days. The minimum brood period from egg to adult emerging was 31 days; the maximum, 304 days.

For central California, Person (*U238*) found that the period from first egg to first emergence averaged 46 days for the first seasonal generation in 1926; 88 days for the second generation; and 243 days for the third or overwintering generation.

In reviewing the results of 3 years of studies, Salman and Bongberg (*U283*) stated: "The variations in the life history that are the result of the influence of temperature are so great that any definite statement of the time necessary to complete the life cycle will be of little use if expressed, without qualifications, in terms of days."

In one experiment Beal (*U6*) succeeded in carrying through development from egg to a single callow adult at a constant temperature

of 93° to 97° F. in 28 days. Although conditions of the test were undoubtedly abnormal, the period is the shortest yet recorded for completion of the life cycle. It probably represents the minimum period during which the western pine beetle can pass through all the stages of egg, larval instars, and pupa, and finally reach the adult form.

Total Brood Production

Several workers studied brood production on hundreds of square feet of bark between 1914 and 1936. They sought to determine the number of beetles needed to attack and kill trees and the resulting emergence under varying conditions and from year to year. The hope was that these counts would show the beetle's capacity to increase, what factors held it in check, and whether the success of brood production could be used to indicate trends of timber mortality.

Keen (*U142*) summarized the results of brood production studies in southern Oregon areas between 1914 and 1926. These studies included 979 trees and 4,177 square feet of bark. The general averages for attack and emergence were:

	Range	*Median value*	*Standard deviation*
Attacks per square foot	1–40	11.6	6
Exit holes per square foot	0–340	63	50

Keen emphasized the great variability in counts of different beetle events and particularly in counts of attacks and emergence. "Attacks range from 1 to 40 per square foot of bark, with a mean usually falling between 6 and 12. It requires the examiation of about 324 square feet of bark to obtain an average attack figure which is accurate within ±1.0. Emergence counts show a tremendous variation, with a range of 0 to 340 beetles emerging per square foot (of bark) with no central tendency or mode. In order to obtain an average emergence with a maximum error of the mean of ±1.0, 22,500 square feet of bark would have to be examined."

Seeking less variable data on normal emergence, to compare with data on cold-weather emergence, Beal (*U11*) counted exit holes per square foot of bark in three areas in eastern Oregon. The samples included 37 trees and 579 square feet of bark. They were restricted to these conditions: a band around the midbole of trees, usually 15 to 25 feet above the ground, showing a normal attack by the beetle; trees of average bark thickness; and trees between 16 and 30 inches in diameter. Enough counts were made on an individual tree so that the addition of 3 more samples did not change the average more than 10 percent. Similarly, enough trees were included so that the addition of 3 more trees did not change the average for the area by more than 10 percent. Usually, 15 to 20 samples were sufficient for each tree and 15 to 20 trees for each area. From these samples, he found that the average number of exit holes for 1930 and 1931 overwintering trees was 112 per square foot, with a standard deviation of 34.

In 1933, 1934, and 1935, Buckhorn (*U37*, *U38*, *U39*) determined emergence on Ochoco National Forest in Oregon. Cages covering 2 square feet of infested bark were placed on the north and south sides of a series of trees at heights of 6 to 8 feet above the ground. Emerging insects were caught in jars partly filled with water and

collected at weekly intervals. The emergence recorded by seasons was:

Season:	*Bark caged (sq. ft.)*	*Total emergence (number)*	*Average emergence per square foot (number)*
1932–33	96	[1] 5,609	58.5
1933–34	132	18,501	140.0
1934–35	120	13,255	110.5
Total	348	37,365	107.3
Total, 1933–34 and 1934–35	252	31,756	126.0

[1] Brood partly killed by the cold winter of 1932–33.

From 1930 to 1934 a good deal of work was done on the Sierra and Modoc National Forests in California in caging bark and determining beetle emergence. Salman (*U270*) summarized these data. From 974 square feet of bark, the average emergence was 111 beetles per square foot. Average emergence by generations varied from 78 to 194 beetles per square foot, and this was considered to be significant of population trends.

Summary of Brood Statistics

All of the work in bark and brood counts has indicated wide variations in beetle statistics. Consequently, few have been tied down within narrow limits. These limitations are recognized, but the best figures derived so far are as follows:

Brood event:	*Basis, sq. ft. of bark*	*Average per sq. ft.*
Number of attacks	4,177	11.6
Number of parent adults attacking	52	25
Inches of egg gallery	—	162
Number of eggs	25.7	648
Number of larvae:		
Overwintering Jan. 1-Apr. 1	927	188
Prepupal Apr. 1-May 1	185	122
Number of exit holes	4,177	63
From restricted sample	579	112
Number of vent holes	1,857	21
Number of new adults emerging:		
Estimated	—	92
From cage records Oreg.	252	126
From cage records Calif.	974	111

A fair general average for normal emergence would be about 115 beetles per square foot. Thus, from an average of 25 beetles attacking per square foot, the normal population increase is roughly 5 times from attack to emergence.

TROPISMS OF NEWLY EMERGED BEETLES

The emerging beetle enters an environment entirely different from that in which it has spent all of its previous existence. From a microclimate in the bark where light and air movement have been largely excluded, it suddenly enters a world of ever varying light intensities, air currents, and odors in the surrounding forest. Relieved of the circumscribed conditions of its larval and pupal existence, it can now of its own volition or in response to stimuli choose the direction it may take in search of food and mate.

Tropisms may have much to do with the time, direction, and distance that beetles fly before attacking another tree. The factors studied most are its response to light, air movements, and attractive or repellent odors.

Light

Gordon (*U74*) studied the tropisms of the beetle and stated: "The western pine beetle is positively phototropic and negatively geotropic." It requires no special apparatus to find that the newly emerged beetle crawls or flies toward the source of light and that usually its first impulse is to move upward.

Early investigators soon found that beetles emerging from a piece of infested bark in the laboratory first moved to the windows. If the beetles did not escape, they remained on the glass or screen for several days. Also, if the outer surface of the infested bark faced the light, the beetles came out through the outer surface as they do from standing trees; but if the bark were turned with the inner surface toward the light, the bettles reversed their normal direction of emergence and came out through the inner surface. If the bark were kept in a container with light excluded, the beetles emerged from both outer and inner bark surfaces, apparently taking the shorter way out.

Experiments with emergence cages placed around trees in the forest have indicated that the movements of the beetle for some days after emergence are influenced by an urge to move toward the light. In several field experiments, Patterson (*U215*), Person (*U238*), and Miller (*U193*), placed cages around the base of standing green trees and liberated newly emerged beetles within the cage. When first liberated, the beetles went to the lighted walls of the cage and showed little interest in the enclosed living trees. They were drawn toward the most intense light even though enclosed under conditions that permitted considerable air movement and freedom to fly toward their natural food. The same tendency was observed by Keen (*U130*). Both Miller and Keen reported that this behavior persisted 3 days. Eventually, however, most of the beetles confined in cages attacked the enclosed trees or logs—after spending several days in an apparent attempt to escape toward the light.

One phase of Gordon's (*U74*) laboratory studies on tropisms indicates that the beetles do not fly unless stimulated by light. About 300 beetles were liberated in a room from which all outside light was excluded. The room was maintained at a temperature of about 75° F., and was lighted by a 75-watt ceiling light. Most of the beetles took flight under these conditions. and it was noted that the flight activity centered around the light. The beetles did not fly directly into the light bulb, but would fly toward it, then past it. The flight was eratic, followed no fixed direction, and was frequently reversed. But most of the beetles flew within a zone of 2 or 3 feet from the bulb itself. When the light was suddenly switched off, leaving the room in total darkness, the beetles could be heard dropping to the floor or striking the walls. When the light was switched on again after a few minutes, all the beetles were resting quietly on the floor, but then, most of them resumed flight. This behavior was verified by Callaham in 1951 (*U46*).

Gordon's experiment explains why we find no record of western pine beetle flight during the night hours, and why no one seems to have found them attracted to night lights near forest areas. We can only assume that during the flight period they spend the night resting in bark crevices or on the forest floor. Observations on trees under attack indicate that the beetles fly to the trees only during daylight hours, beginning soon after sunrise.

These observations all point to a very positive attraction to light by newly emerged beetles. However, no one seems to have taken the time to determine the reaction of the western pine beetle to light during the pre-emergence period. Hensill (*U98*) tested the light tropism of mountain pine beetle adults that were removed from logs before they had emerged naturally; he found that they were negatively phototropic to a marked degree. Callaham (*U45*) found that the Jeffrey pine beetle was similarly negatively phototropic when adults were prematurely removed from their pupal cells. It is altogether probable that the immature adults of the western pine beetle possess the same response, since the avoidance of light would seem to be one of the factors that cause them to remain in the bark until they are fully matured and ready to emerge.

Whether mature adults of the western pine beetle are attracted to light until the time they are ready to start new attacks was tested by Struble (*U302*). In this experiment trap logs were exposed to the attack of beetles confined in a laboratory room. The light intensity for each log varied according to the distance from fixed windows. He found that the heaviest attacks occurred on logs near the windows which received the greatest amount of light. Logs in the darkest locations drew only a very slight attack, but some attacks did occur on all logs regardless of their location.

Air Currents

Gordon (*U74*) conducted one experiment with his olfactometer in which he tested the reaction of the beetles to air movement alone. This test was carried out under conditions in which the beetles could move only by crawling, since the air space in the apparatus did not permit free flight. "A preliminary test with 180 beetles showed that 138 went against slight air currents (3 liters of water suction per hour). However, when the air current was appreciably increased above this value, contradictory results were obtained."

Callaham (*U46*) studied the olfactory and air-current tropisms of the western pine beetle at Placerville, Calif., in 1951 by using a specially designed wind tunnel. He found that with wind velocities of one-half mile per hour or more, the bettles fly with the wind, and are unable to fly against it even in response to their strong phototropism.

Such field observations as have been made do not shed much light on the response of the beetles to air currents. Keen's observations (*U131*) were that the beetles followed the direction of the wind. Evenden (*U59*) and Person (*U238*) do not mention air movement in their observations on flight, but Person states that the beetles took flight always in one direction; obviously this tendency could be due to other stimuli than air currents.

The general movements of populations in pine areas, as indicated by the location of infested trees, do not show a tendency on the part of the beetles to fly always with the prevailing winds. This is to be expected if odors are a dominant factor in drawing the beetles to the trees that they attack. It has been found that flight movements of the beetle are short and spasmodic. As winds usually change direction or die down within a 24-hour period during the flight season, they probably do not greatly interfere with the beetles' direction of flight or the distance covered.

Odors

Beetles apparently do not attack trees indiscriminately, but, regardless of the source of light or the direction and velocity of air movements, avoid some trees in order to attack others. This observation has led to the assumption that responses to odors are a dominant factor in the beetles' selection of trees. If selection is a chemotropic response, then the beetles can detect the odors of certain attractive trees. Such odors might well be too faint to be detected by the human sense of smell, but still be recognizable to a highly developed olfactory sense of the beetle.

After a tree has been attacked, it has a characteristic odor that can be detected by humans. An experienced spotter could often find freshly attacked trees by this characteristic pungent odor.

Study of olfactory responses was stimulated by the theory that if the chemical nature of this attraction could be identified, then it should be possible to put the responses of the beetle to good use in control measures. Further, if the odor could be produced synthetically then it should be possible to attract the beetles to artificial traps in the forest. This possibility led to a series of studies and experiments dealing with attraction.

Results of Attraction Studies

The Ashland Studies, 1916

As early as 1916 the types and condition of trees infested by western pine beetle were studied near Ashland, Oreg. In a summary of his work Keen (*U127*) reported a variable degree of selection of fallen trees (windfalls), trap trees (recently felled), top-killed trees, trees infested by the California five-spined engraver (*Ips confusus*), and healthy trees near weakened trees. Top-killed and engraver-infested trees were most often attacked: 26.6 percent of the top-killed trees from which the top-killing insect had emerged, and 26.2 percent of the trees still infested by the engraver were attacked by the western pine beetle during the season. This was a much higher proportion attacked than among standing trees not top-killed and was considered to indicate a definite attraction to trees recently top-killed by engraver beetles.

The Cascadel Studies, 1926–27

Person (*U238*, *U241*) started attraction studies in 1926 on the Cascadel area near North Fork, Calif. His first approach was entirely empirical, pointed toward finding evidence that the beetles

were being attracted to certain materials or to trees under varying conditions. He had already established that the beetles selected the slower growing trees in the stand, and he developed the following leads during the 1926–27 season:

Trap trees.—Beetles were readily attracted to and attacked freshly felled trees (traps) in one case, but failed to attack in another. Factors governing attraction to trap trees appear to depend upon time of cutting, location, and characteristics of the tree itself.

Top-killed trees.—Trees previously top-killed by engraver beetles were found to be attractive to the western pine beetle. Of 176 ponderosa pines top-killed on the experimental area in 1924–26, 43 percent were attacked by the western pine beetle within 2 years after top-killing.

Artificially topped trees.—A series of 20 trees were artificially topped; a few of these attracted the red turpentine beetle (*Dendroctonus valens*), but none were attacked by the western pine beetle. Artificial topping, therefore, seems to differ from *Ips* top-killing in its attraction to the western pine beetle.

Girdled trees.—A vigorous tree was girdled at breast height by removing a 2-foot band of outer bark, phloem, and cambium to the depth of the sapwood. This tree did not attract the western pine beetle until the second season after girdling, when it was attacked and killed.

Trees attacked only at base under cage conditions.—Beetles were attracted to both susceptible and resistant trees on which an attack was artificially induced. This was demonstrated by a series of cage experiments in which 10 to 15 feet of the lower bole was screened in and adult beetles were introduced and forced to attack within the cage. In all cases, other beetles flying in the area were attracted to the tree and attacked it above the cage.

Roots injured by pruning.—Two fast-growing trees that were heavily root pruned attracted red turpentine beetles, but did not attract the western pine beetle the first year after injury. Attractiveness for subsequent attack would be complicated by the effect of reduction in growth rate.

Lightning scars.—The observation that lightning-struck trees were usually attacked by the western pine beetle suggested that this attraction might be due to the result of overheating phloem and cambium. Four trees were therefore artificially scarred to simulate lightning injury. A scar 2½ inches wide extending from a point near the top of the trees to the base was made on each tree. Two trees were slow-growing and two fast-growing. Two of the scars were scorched with a blowtorch. None of these artificially scarred trees attracted the western pine beetle, but a few red turpentine beetles did attack one of the trees near the base. On the other hand, a group of 3 trees within 100 feet of the experiment were attacked and killed; therefore, the scarred trees did not escape because of lack of beetles nearby.

Fire injury to foliage.—In April 1927 just before the flight period, 9 trees were artificially scorched to produce varying degrees of injury to the foliage. None of these attracted the western pine beetle until September; then 2 trees that had been 100-percent defoliated were attacked and killed. This experiment confirmed the

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conclusion from other studies that the odor of smoke or of recently fire-scorched trees does not attract the western pine beetle. Rather, reduction of growth as a result of fire injury attracted the beetles to severely defoliated trees within a year or two after the injury (see p. 224).

Pitch masses.—The fire-injury studies suggested that the pitch flow produced by attacking beetles was the source of attraction. Pitch tubes were then transferred from an attacked tree to three selected unattacked trees of slow growth rate. Two new attacks were made near the pitch masses on one of these trees, but the attacks were unsuccessful. In 1927, pitch tubes were placed on a very slow growing tree, and it was later attacked. The general results indicated that pitch masses may have some attractive influence, but that it is too slight to be of great significance.

Beetles boring in phloem area.—It was next considered that the attraction might be due to the presence of adult beetles working in fresh pitch flow. Therefore a nail hole extending into the phloem was made in selected trees and beetles introduced; about 20 percent of them attempted to extend egg galleries into the trees but were unsuccessful. In one slow growing tree, attacks through nail holes were followed by a successful attack over the entire bole from beetles flying in the area; but here again there was a question whether the general attack had been induced or would have occurred anyway.

Concentrations of beetles.—Studies were made to determine the attraction of a large concentration of adult beetles to other beetles flying in the vicinity. This was done by observing evidence of attraction to emergence cages, where large number of beetles were confined, and to adjacent uncaged trees. No evidence of such attraction was found.

The Modoc Studies, 1928–29

In 1928 the Cascadel attraction studies were transferred to Modoc National Forest in California, to carry on the project in an area where there was an active epidemic infestation and large areas of susceptible timber. During 1928–29 a comprehensive series of experiments were carried out to determine the attraction of the beetle to different parts of the trees, to slow growing as compared to fast growing trees, and to various chemical substances. Chemotropic responses of the beetle were studied, as were changes that take place in the sugar concentrations of the bark and phloem preceding and subsequent to attack.

Mirov (*U211*) made an intensive study of the reactions of the beetle to attractive and nonattractive materials. A large screen insectary was constructed for this study. The beetles were reared in large numbers in separate cages and then liberated in the insectary. Specially devised traps in the insectary caught the beetles coming to attractive materials. Mirov's report reviewed the literature of previous work that had been done on the chemotropic responses of insects, in addition to presenting a number of significant conclusions developed by his own experiments with the western pine beetle. Among the latter were the following:

It was soon found that insulation, relative humidity, and temperature play a very important part in attraction studies.

(Especial measures were taken in the insectary experiments to compensate these factors.)

Dendroctonus brevicomis is positively chemotropic towards *Pinus ponderosa* and is attracted by odoriferous substances emanated by its host tree.

Sugars present in the phloem of *Pinus ponderosa*, and probably products of their decomposition, have been found to be more attractive than essential oils of bark and wood. Essential oils of needles proved to be non-attractive to this beetle.

Fermented phloem proved to be the most attractive of all the materials used.

It has been found that there is quite a pronounced preference in the olfactory response which *D. brevicomis* shows toward slow growing trees, especially to the phloem. This item needs further study.

Mirov did not continue his attraction studies, but Person and Jeffrey developed further phases. Jeffrey's work (*U107*, *U109*) on phloem and bark sugars showed that the concentration of reducing sugars—particularly levulose—is higher, and that the sucrose concentration is lower, in the slower growing attractive trees than in the faster growing less attractive trees (fig. 9). When a tree is felled, changes in sugar concentration set in, such as would be associated with fermentation. This is followed by a rapid decrease in sugars, evidently caused by respiratory fermentation produced by micro-organisms (fig. 10). Jeffrey states (*U107*):

> It is not intended to suggest that the actual hydrolysis of sucrose to reducing sugars in either the standing slow-growing tree or the felled log would actually attract beetles. It is a definite possibility, however, that some other change associated with or following this change might produce a volatile substance which would be directly attractive to the beetles.

FIGURE 9.—Relation between radial growth rate of ponderosa pine and the concentration of certain sugars in the living bark.

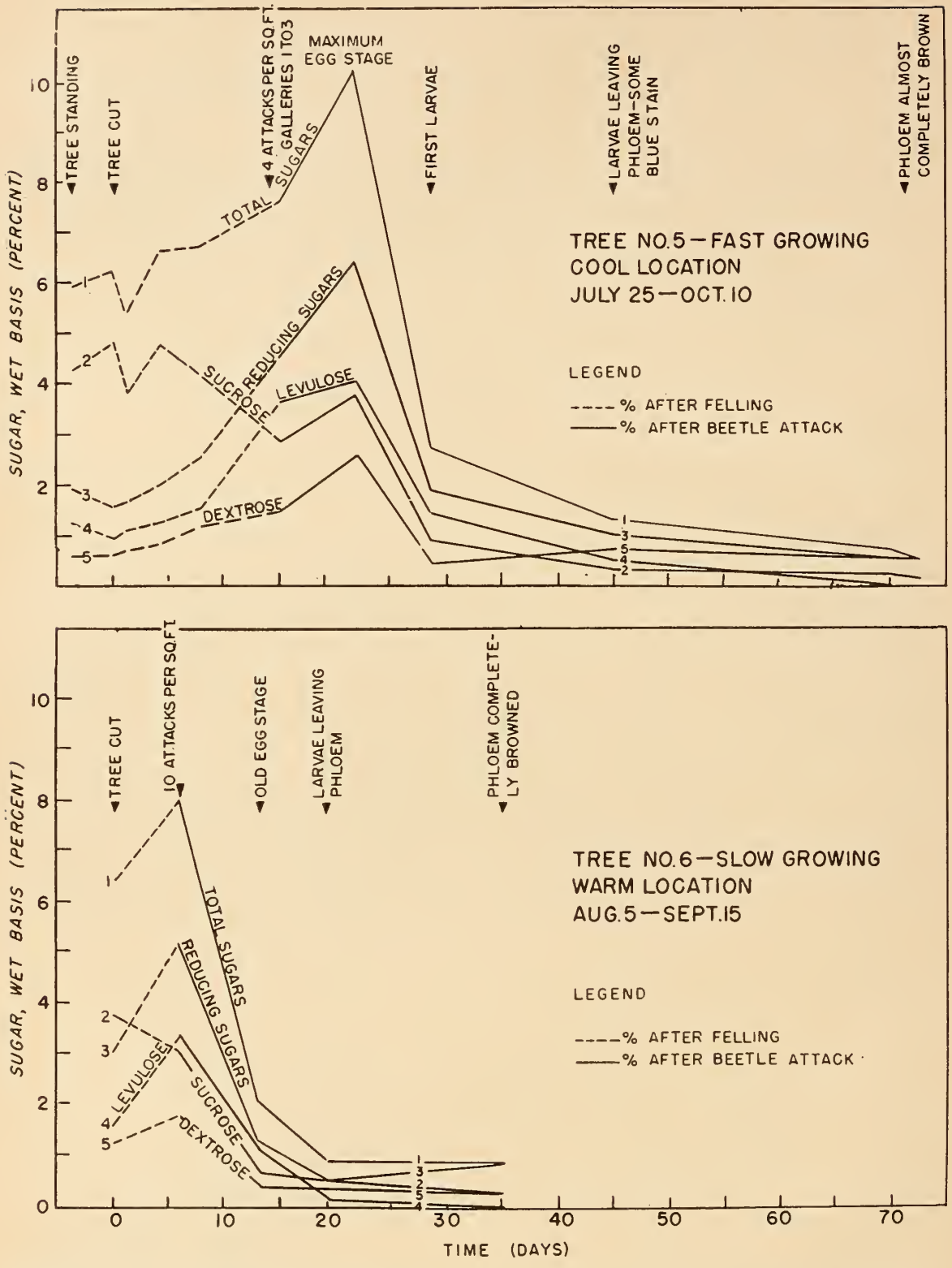

FIGURE 10.—Changes in concentration of certain sugars in the living bark of ponderosa pine after felling and western pine beetle attack.

Still another line of attack upon the factors involved in attraction was the relation of hydrogen ion concentration or pH, in pine phloem to bark beetle attack. Durbrow (*U53*) explored this field by comparing the pH in trees from different vigor classes to see if there was any correlation between pH and bark beetle attack. The study did not get much farther than working out the technique for determining the hydrogen ion concentration in the phloem, and very little was established to show that this is an important factor in the attraction of bark beetles. Durbrow's conclusion was that "ap-

parently pH is not a satisfactory index to the health or attractiveness of trees." However, in spite of the small amount of data, he summarized the results as follows:

1. A pH below normal at the time of attack on trap logs.
2. A tendency for trees to approach this attractive pH during the season following injury.
3. An increase in pH shortly following attack and during the development of broods.
4. No relation between rate of growth and the pH of the inner bark.
5. A change in trap logs away from the normal and toward the acid side of the range.

Person (*U245*) summarized the results of all this work; these were stated as tentative conclusions:

1. The inner living bark is the most attractive major part of the tree; the outer bark ranks second, the sapwood third, and the needles are the least attractive of the parts of the tree that were tested.
2. No consistent difference was found in the attractiveness of slow and fast growing trees, as a whole, after being felled.
3. The attractiveness of a tree increases almost immediately after being felled. The degree of attraction apparently increases for a few days and then decreases.
4. Fermenting inner bark, if comparatively fresh, is the most attractive of the substances tested.
5. Turpentine and bark oils distilled from western yellow pine are apparently neither attractive nor strongly repellent. Mirov found that some of these oils were much more repellent than others, and that the lower the boiling point, the less attractive the oil.

Olfactometer Experiments, 1933

Gordon (*36*, *U74*) attempted to study the chemotropic responses of the beetle in 1933 by means of a specially designed olfactometer (fig. 11). He tested a wide variety of chemical materials, with results that can be accepted only so far as the olfactometer gives a reliable measure of the responses of the beetle. Most of the chemicals tested were repellent, and the pyridine and pyrrole derivatives were highly repellent to the western pine beetle. However, two terpenes, linalool and laevo-menthyl acetate, were slightly attractive.

The most positive result was an attraction to freshly fermented phloem of ponderosa pine. Gordon found the phloem to be repellent the first 2 days, but attractive after the third day. Phloem became highly attractive on the seventh day. Then the attraction declined. At the end of 20 days of fermentation, the phloem was highly repellent. This work confirmed Mirov's (*U211*) results. Gordon, however, continued the fermentation until it began to break down into acetic acid, which may explain the highly repellent action after 20 days.

Gordon (*36*) concluded that (1) felled trees are always attractive, (2) some standing trees of a given species are more insect resistant than others, and (3) an initial attack may increase in intensity, presumably because of a stimulation by the production of attractive substances.

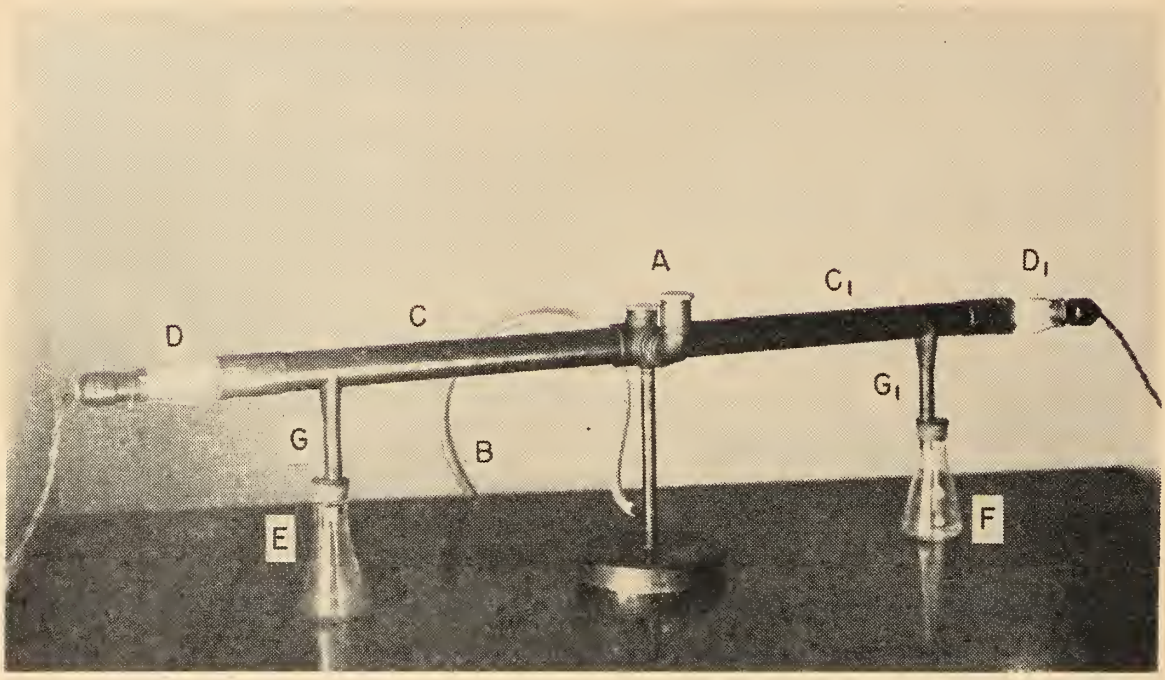

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FIGURE 11.—Olfactometer designed by A. Gordon for testing chemotropic responses of the western pine beetle: *A*, Valve opening for introduction of beetles; *B*, air suction hose; *C* and C_1, tubes of equal length; *D* and D_1, lights of equal intensity; *E*, flask with test material; *F*, empty flask for check; *G* and G_1, air inlets.

Person's Tree Selection Theory

Although the attraction studies did not produce results that led to application in direct control, they did lead to formation of a theory to explain why the beetle selects certain trees. This theory has at least served as a background for later studies on the character of susceptible trees. Person (*112*) explained what attracts the beetles to certain trees as follows:

> The initial attraction of beetles to a tree is due to the formation and escape of volatile aldehydes or esters which are a by-product of a respiratory fermentation resulting from abnormal enzyme activity in subnormal trees. The causes of this subnormal condition may be drought, injuries of various kinds, or something else that interferes with the normal physiology of the tree.
>
> This initial attraction, particularly in trees only slightly subnormal, is probably so weak as to be detected only by beetles in the immediate vicinity of the tree. But after a few attacks are made a second, stronger attraction is started by the yeast introduced by the attacking beetles, finding the inner bark a favorable medium for its growth. This secondary attraction is probably strong enough to attract beetles for a considerable distance, with the result that the tree is usually heavily attacked and killed.

Although this theory is yet to be proved, it is a most logical explanation for attraction of beetles to susceptible or high-risk trees. However, in sanitation-salvage logging, which has since come into use as an indirect control measure, the selection of high-risk trees is based on recognition of visual crown characters and not on odors emanating from the trees. Callaham's (*U46*) study of olfactory tropisms, though conducted in specially designed apparatus,

found no significant attraction to or repulsion by fermented phloem or certain oleoresins, but he considered the results inconclusive because many factors could not be controlled. Until some means can be devised for detecting the esters to which the beetles respond, Person's (*112*) theory of tree selection will continue to be the accepted explanation of attraction.

PREFLIGHT HABITS

What beetles do immediately after emerging from the bark is of particular interest when considering the possibility of killing them by contact sprays before they take flight.

Evenden (*U59*) was the first to describe an emergence, one he witnessed near Coeur d'Alene, Idaho, in 1916:

> Contrary to my expectations, the beetles do not remain upon the outside of the host plant for any length of time. This may be due to the fact that the day on which this record was taken was very warm. Upon emerging from the bark, the beetles rest for a few seconds, 5 minutes being the maximum length of time; then after raising their elytra for a few times and apparently testing their wings, they took flight in different directions. Many of them return to the host tree for a few minutes.

Person (*U238*) also carefully recorded his observations of the beetles' preflight habits as noted at Cascadel on Sierra National Forest, Calif., in 1926:

> The newly emerged beetles usually crawled about in search of an exposed point before attempting flight. They then spread and folded their wings a number of times and then took off. In many cases the attempt failed and the beetle fell to the ground, crawled back to an exposed point of bark and tried again.

Moore (*U213*) reported on the behavior of five western pine beetles which emerged from logs that were kept under close observation for 13½ hours. He found that the minimum length of time that any adult would remain in contact with the log after emergence was 60 seconds.

FLIGHT HABITS

Once the beetle takes flight, its actions are hard to follow. An adult is a very small, dark object and flies with a swift, irregular, darting movement. No observer has been able to follow an individual beetle in flight more than about 100 feet from the brood tree. Beetles have been seen only just as they are leaving the brood tree or when coming in to make their attack. As a result, we know little about the beetle as it flies through the forest in search of new trees to attack. Just what it does during the greater part of the flight is a mystery that has intrigued many observers for many years.

Field Observations of Flight Behavior

In 1916, Keen (*U131*) carried on a long series of observations and experiments at Ashland, Oreg., dealing with flight habits. He studied the reactions of adult beetles in flight by rearing a large number in an insectary and liberating them in the forest at a fixed

point. At each point of the compass, he set up tanglefoot screens 25 feet from the liberation point. These consisted of frames of window glass, 2 by 3 feet, on which tanglefoot solution was smeared. His results show:

> They invariably followed the direction of the wind. After leaving the liberation board, they generally circled somewhat to gain elevation. If the breeze was at a lull, they would rise to a considerable height, 25–30 feet, and then caught by the breeze would be carried away by it. Beetles could only be followed by the eye for a distance not greater than 100 feet. Hundreds of beetles when liberated were observed to fly towards the frames, and then rise and fly over or around them, showing that they do not fly blindly into such an obstacle.

Person (*U238*), after observing beetle flight at Cascadel in 1926, stated:

> When successful [in taking flight], beetles flew off in a north or northeast direction, in the cases observed, at an angle between the horizontal and the perpendicular. The flight could be observed for a distance up to 100 feet, and in every case the beetle flew past the nearby trees with no evident intention of attacking.

Effects of Air Temperatures on Flight Behavior

These experiments and observations were carried on under temperatures that permitted normal activity of the adults. (Miller (*95*) records the range of active temperatures for adults as from 45° to 95° F.)

Person (*U238*) checked the flight behavior under varying air temperatures in the field. He states:

> The optimum temperature for the beetles was found to be between 70 and 85° F. Beetles moved about actively, but normally in the sun at temperatures up to 85°. Many of them made successful attempts to fly. Between 85 and 95° the beetles were abnormally active and inclined to avoid the full sunlight. Their movements were hurried and attempts at flight were usually unsuccessful. Temperatures over 95° were too hot for the beetles. They avoided the full sunlight, and when exposed to it they hurried wildly about and often lost their footing and rolled into a bark crevice. Attempts at flight were usually unsuccessful. One beetle that failed to get out of the sun soon enough became dormant and died in about 3 minutes at 102° F.
>
> These temperatures were taken on the bark surface where the beetles were found, with a corrected Eastman thermometer. Since the black beetles would absorb the heat rays of the sun, their internal temperatures would be considerably higher than temperatures at the surface of the bark.

Beal (*U6*) observed the behavior of adult beetles under a fairly wide range of temperature. He found that at 36° F. adults were capable of slow movements of the legs but were unable to walk. At 48° to 50° they could walk slowly; above 50°, activity increased with temperature. Adults were "very active" at 84° to 88°. Adults exposed to constant temperatures at 93° to 97° were "all dead at the

end of 4 weeks" although they were kept in the natural phloem where they could feed.

Thus, the optimum temperature range under which adult beetles can sustain flight is between 70° and 85° F. When temperatures drop below 50°, adults presumably cease flight and rest in some sheltered place. Temperatures above 95° are too hot for beetle activity in exposed places.

Influence of Weather During the Flight Period

Weather conditions during the flight period may limit or completely override any inclination of beetles to move in a given direction and may at times have a decisive effect upon the dissemination of the species. Conditions most likely to affect beetles at this time are wind, temperature, and unseasonable storms.

Wind effects on dissemination are not clear. The beetles are able to fly either with or against air movements of low velocity and hence can respond to other factors, such as light or attractive host material. On the other hand, if beetles are caught in flight by winds of moderate or high velocity, it seems probable that they would be carried in the direction of the prevailing air movement. However, there is no conclusive evidence one way or the other on this point, except that general dispersion of beetles throughout an area goes on regardless of wind and air movements.

Temperatures within the range of beetle activity are an essential requisite to flight. Sudden drops in air temperature to 50° F. or lower will arrest all flight movement until higher temperatures return. Therefore, a prolonged cold spell during the flight period can break the force of an attack.

Unseasonable storms accompanied by precipitation and low temperatures would most obviously interfere with the flight of beetles. Late spring storms that come during emergence or early storms in the fall not only stop flight movements, but may result in a high mortality as well. One such case was reported by Gustafson (*U77*) on the Sierra National Forest:

> The exceptionally late flight, ending December 11, 1932, was dissipated by the sudden cold weather and snow storm of December 12 to 17. This sudden drop in temperature, followed by a severe snow storm, caught many of the broods in full flight and they were consequently destroyed before they could secure protection by boring into the bark.

Furniss (*U68*) records a similar arresting of the emergence and flight of beetles by cold weather in the late spring of 1934.

Another possible influence upon dissemination is the effect of dark, cloudy weather. All observations of beetles in flight in the field seem to have been made in bright, sunny weather. It is doubtful whether the beetles do much flying on dark days, even though temperatures are favorable, since the light stimulus is greatly reduced.

Swarming Habits

Webb (*144*) stated that the beetle "attacks the living trees in swarms." He probably intended to convey the idea that they

attack in great numbers. No subsequent western pine beetle investigation records a tendency of adults to move concertedly in masses, as do bees, termites, and grasshoppers. Flight is apparently an individual activity for each beetle. As they fly, they respond to certain stimuli and attractions, but these influences do not cause them to move in mass flights. Anything resembling true "swarming" in flight is yet to be recorded.

Duration of the Flight Period

The time between the emergence of a beetle from its brood tree and its entrance into the bark of an attacked tree is obviously important to the survival of the insect. During this period the beetle does not feed, and it may be exposed to unfavorable weather, predators, or other adverse factors. Its chances of meeting an untimely fate are multiplied as the flight period is extended. One would expect the beetle to attack a tree as soon as possible in order to reach the shelter of the inner bark where it finds food and mate and where many of the factors unfavorable to its existence are excluded. But since it has been quite impractical to follow the course of individual beetles, we have only indirect evidence as to how long they spend in flight.

We know that the beetles do not all emerge at once, and that flight continues more or less throughout the season. However, there are well-defined peaks of emergence and peaks of attack. It can be safely assumed that flight activities occupy much of the time between these two peaks. Keen (*U130*) approached the question of the length of the flight period by comparing the peak periods of emergence and attack near Ashland, Oreg., in 1915 and 1916. He found that "from the plots showing quantity of emergence and quantity of attack on different dates, it would appear that maximum attack followed maximum emergence by 26 days."

Keen also found that caged beetles confined with a trap log "were capable of attacking 3 days after emergence"—an interval confirmed by several subsequent caging experiments. However, it cannot be expected that beetles in confinement would follow the same behavior as beetles that have full freedom of flight in the forest. Under natural conditions, the evidence all indicates a period of at least a week or two after emergence when most of the beetles are either in flight or resting somewhere in the forest before they finally select and attack new trees. This period may be shortened or prolonged by weather conditions and season.

Distance of Flight

Webb (*144*) made the following observations:

> After leaving the tree or trees in which they went through their transformations the beetles fly away to find trees in which to deposit eggs. They may select trees close at hand or may fly quite a long distance before making a selection.

This observation has not been changed materially by subsequent studies of flight behavior. But how far is "quite a long distance"?

This is the question that has absorbed most of the attention in flight studies. It is important because the distance that beetles may fly must be considered in setting the boundaries of control areas.

Keen (*U131*) first attempted to arrive at some conclusions as to flight distances by deductions from field data bearing on distances between trees infested by succeeding generations. He observed that after the beetles emerged from an infested tree, a new tree would often be attacked soon afterwards in the general vicinity. On the basis of such records, he inferred that the beetles do not travel very far. "The distance of flight averages probably less than 100 yards." Other investigators and spotters on early control projects arrived at the some conclusion by the simple process of noting the distances between recently abandoned and newly infested trees.

This method of establishing flight distances by inference was admittedly inconclusive. The fact that a newly attacked tree is found relatively close to a recently abandoned one might merely indicate that the beetles in the surrounding area were being attracted to this particular site because they found here a susceptible tree and favorable environment. In commenting on these first observations on flight habits, Dr. A. D. Hopkins stated in a letter:

> There is no doubt that all of the *Dendroctonus* beetles can and do fly long distances from the trees in which they have bred, and that they are attracted to certain trees and centers from all directions. There is, therefore, no way of securing facts or evidence to prove where all the beetles come from that attack a tree near one from which the broods of a preceding generation have emerged.

Experiments With Marked Beetles

Keen (*U131*) tried to establish unquestionable records of the source of beetles coming to a newly attacked tree. To do this he proposed to mark a large number of beetles after emergence so that they could later be identified, liberate them from a fixed center, and then see if any of these marked beetles could be recovered from trees attacked near the liberation point.

After repeated experiments, a practicable marking technique was developed with rosalic acid dye dissolved in 95 percent alcohol. The solution was applied to the beetles in the form of a mistlike spray that dried very quickly. This application caused no apparent injury to the beetles and remained fixed even after the beetles had extended their egg galleries into the resins and water-saturated tissues of the inner bark of trap logs. Beetles so marked could be identified by a color reaction when they were dropped into a testing solution of sodium hydroxide even though they had received only a few droplets of the solution.

The liberation phase of this experiment was carried out in the spring of 1917. Infested bark was collected from seven trees that made up all of the overwintering infestation on a mile square section of the Lamb's Mine Unit. The beetles from this infested bark were reared and allowed to emerge in an insectary; here they were marked and then liberated at a central point in the same section

from which the bark was collected. A total of 8,000 marked beetles were liberated between June 15 and June 29.

No new attacks appeared in this section until August 13, when a newly attacked tree was found about one-fourth mile from the liberation point. The tree was felled and the parent adults collected from their egg galleries in the inner bark. They were preserved by drying. The experiment was interrupted by Keen's enlistment in the Army and it was not until October that Miller (*U179*) tested the marked beetles. He reported that 181 out of 1,400 attacking adults collected from this tree gave a slight reaction in the testing solution, indicating that they had been marked. The remaining 1,219 beetles gave no reaction and had apparently come to the tree from some other source than the liberation point.

The results, insofar as they can be accepted, serve to confirm Hopkins' statement (p. 51). Although some of the marked beetles traveled one-fourth mile to attack a new tree, they were joined in this attack by many other beetles from some unknown source. What became of the remaining 7,819 marked but unrecovered beetles that were known to have taken flight from the liberation point and how far they may have traveled before attacking is still a mystery. This experiment is the only known attempt to trace marked western pine beetles from the point where they took flight to the tree that they attacked.

Experiments With Trap Trees

Patterson (*U215*) tried to obtain positive records of flight distances by creating attraction centers at fixed distances from known sources of emerging beetles. In one of these tests near Ashland, Oreg., he forced an attack on the base of a living tree by confining newly emerged adults in a cage enclosing the lower 8 feet of the trunk. Before the start of this attack, all infested trees within a radius of one-fourth mile of the caged tree were cut and the bark burned. Soon after attack started in the cage, beetles from outside sources attacked the entire trunk. These beetles were considered to have come from beyond the treated area, which would have necessitated a flight of at least one-quarter mile.

Trap trees felled at isolated points during the flight season have been used as another method of determining how far beetles may fly. Miller (*U187*) reported a record in 1918 of a trap tree, on the lower fringe of Sequoia National Park, successfully attacked when the nearest tree from which the beetles were considered to have emerged was 1.2 miles distant.

Patterson (*U216*) also used trap trees in an isolated grove of pines in the Rogue River Valley to obtain a record of long-distance flight. This grove, which contained no bark beetle infestation of any sort when the trap was felled, was surrounded by an area void of pine. The nearest known bark beetle infestation was 2 miles distant. The trap tree was felled on August 19, and by September 15 western pine beetles and associated insects were attacking the log and stump. These beetles had flown at least 2 miles to reach the trap, but the trap-tree studies do not prove that the general population flies this far.

Records of Minimum Flight Distances

It is equally important to know whether some of the emerging beetles make relatively short flights and attack trees near the point of emergence.

Miller and Person (*U205*) shed some light on minimum flight distances in their work near North Fork, Calif., from 1921 to 1923. They attempted to introduce the western pine beetle into an isolated grove of ponderosa pine some 3 miles from the main pine type and about 1,000 feet lower in elevation. Trees in the grove, occupying a favorable stream-bottom site and all making vigorous growth, covered about 1 acre and were surrounded by grass and brushlands. No trees in the grove had been attacked by bark beetles for many years, if at all.

Felling a trap tree in 1921 failed to attract beetles. Next, infested bark was placed in the grove in April 1922; 22,590 beetles emerged, but again the experiment failed to result in successful attacks on the living trees. However, 492 pitched-out attacks were found on 1 tree around which most of the infested bark had been piled. A similar planting of infested bark in August 1922, brought similar results. In April 1923, infested bark was planted again and this time a trap tree also was cut. Out of 3,000 beetles emerging from the bark, about 500 went to the trap tree and successfully attacked it. No living trees in the grove were attacked.

Aside from demonstrating that the western pine beetle could not be artificially established in the fast growing trees on this low-elevation site, the experiments also indicated that only a very small percent of the beetles attack near their emergence point—even when suitable host material, such as a trap log, is available. Most emerging beetles apparently left the grove, even though their flight carried them into nontimbered territory where there were no pines to attract them.

Person (*U238*) obtained further data on minimum flight distances in 1926, by building up an emergence center within the main pine belt. The site selected was free of infestation but contained several trees of low vigor that were considered susceptible to attack. It was expected that the beetles would be less likely to leave the point of emergence if susceptible trees were available. Although one tree was successfully attacked on the site where the infested bark was piled, Person's conclusions as to flight habits were: "Only a very small percentage of the emerging beetles attacked the tree at which the bark was piled."

To sum up, the experimental evidence indicates that some beetles may attack only a few feet from the point of emergence and others may fly as far as 2 miles. However, the results support the theory that emerging beetles tend strongly to move away from the vicinity of the trees in which they are reared, and that this tendency predominates the attraction of food material such as susceptible trees and traps.

Average Flight Distances in Population Movements

Still another question important to control operations is the movement of large populations. An area cleaned of infestation would become reinfested much more quickly by the mass movement

of beetle populations from adjoining infested areas than by long flights of a few beetles coming into the area. A series of experiments conducted from 1924 to 1934 were designed to determine the average flight distance of large numbers of beetles.

The Forked Meadow Flight Study, 1924

Miller and Person (*U207*) in 1924 studied the rate at which a small unit may become reinfested from outside sources after all of the infestation that could be detected within the unit had been treated. All infested trees were located on the Forked Meadow Unit, of Sierra National Forest, Calif., a circular area of 3,200 acres, roughly 1¼ mile in radius and forming a natural watershed, and these trees were treated by continuous control work throughout the season. The area was surrounded by pine type, and within a border zone one-half mile wide, the location and emergence period for all infested trees were recorded so that the nearest source of possible infestation was established.

New trees were attacked in the control area about as fast as the infested ones were treated. The infestation within the control unit actually increased during the season despite the control work. This was also true in the border zone where infested trees were left untreated. In general the season of 1924 was one of increasing infestations everywhere, and the Forked Meadow Unit was no exception to this trend. After the distances between recently abandoned and newly attacked trees on the experimental area had been measured, it was concluded that "the average distance from trees attacked to the nearest tree from which beetles could have come was less than ½ mile and did not exceed 1 mile at the maximum."

The Oat Mountain Experiment, 1925

In 1925 Miller (*U192*) again tried a similar test under conditions requiring longer flight distances. This time he selected a peninsula of pine type that extended about 2 miles from the main pine type of the Cascadel Unit. Known as the Oat Mountain area, it contained about 2,500 acres. On three sides (southeast, southwest, and northwest), the pine type was bordered by brush and grass areas extending several miles. It was assumed, therefore, that the beetles reinfesting the Oat Mountain area after it had been thoroughly cleaned of infestation could come from one direction only, northeast.

All of the 1924 overwintering infestation that could be detected on the Oat Mountain area was treated in the winter and spring of 1925. This operation left a clean area for the beetles to invade during the flight period in 1925. All trees from which beetles emerged within a mile of the control area were mapped, and the control area was cruised several times during the season to locate the new attacks. By the end of the season, the beetles had spread over the Oat Mountain area so that the distribution of the infested trees corresponded fairly closely to that preceding control.

Miller (*U195*) concluded: "This spread represents a flight of 1½ miles at the minimum and 2 miles at the maximum." The assumption that the beetles made long distance flights was supported by the fact that a group of three large trees was attacked at the

extreme southern end of the peninsula: "The flight to these trees could not have been made by a few beetles attacking by mere chance, but must have been controlled by a definite attraction which drew the beetles in large numbers for a considerable distance."

Yet this and the Forked Meadow study were not conclusive; the experimental areas were not completely isolated by type barriers. Although it could be claimed that the beetles had traveled 1 to 2 miles to reach certain trees, there was no assurance that they did not start their flight from trees much farther away in untreated adjoining areas. What seemed to be needed were experiments in a completely isolated area, separated on all sides from other infested areas by wide breaks in the pine type.

The Devil's Garden Flight Study, 1928–33

Complete isolation was sought in the Devil's Garden Extermination Experiment (see also p. 321). Timbered Mountain, on the Devil's Garden plateau, Modoc National Forest, Calif., is about 6 miles from the nearest large area of pine type (fig. 12). A few widely scattered pine trees grew in the intervening juniper type, but no beetle infestation could be found in these isolated trees. Complete eradication of western pine beetles was attempted on Timbered Mountain.

In summarizing data on the flight phase of this study, Johnson (*U121*) reported that most of the new attacks during the control period were concentrated in the center of the area and toward the

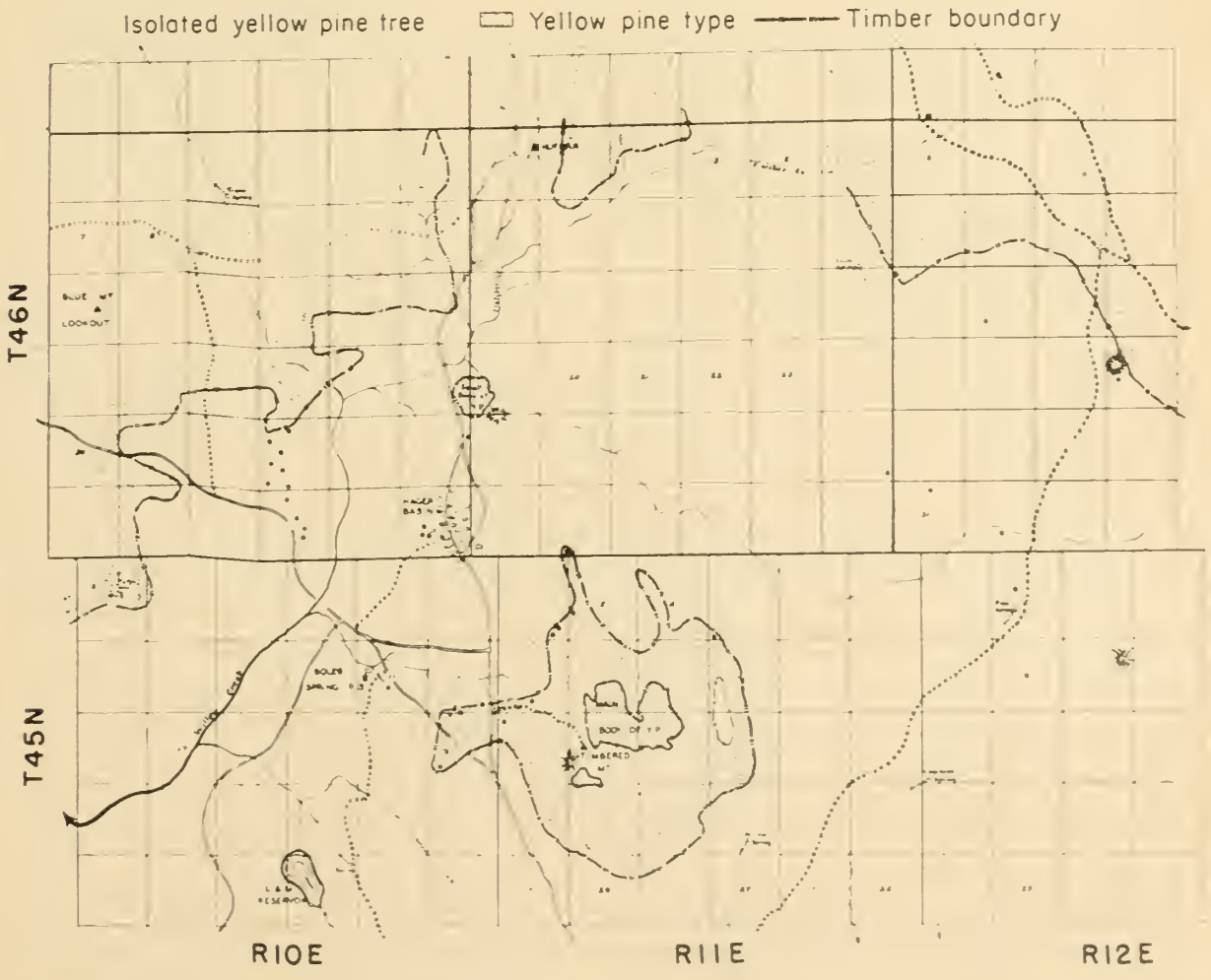

FIGURE 12.—Devil's Garden experimental area, Modoc National Forest, Calif.

southern, southwestern, and southeastern boundaries. In these directions the nearest areas of pine type were from 12 to 30 miles away. On the northern part of the area, which was separated from other bodies of pine timber by a gap of only 6 miles, there were practically no new attacks. Johnson concluded: "There is no evidence of beetles flying into the extermination area from surrounding pine stands several miles away. The continued bark beetle activity on the extermination area has come from within the area itself."

This was the last attempt to determine the flight distances of the western pine beetle by experimental methods; it, too, failed to yield conclusive results. The study did serve, however, to emphasize the important role of associated insects. It was fairly obvious that the western pine beetle can maintain limited populations in small bark areas of trees infested with flatheaded borers or other associated insects without being detected. If this is the case, then complete eradication is impossible unless all of the associated insects are also exterminated. The problem is further complicated by the presence of windfalls and injured trees which are difficult to find. It is doubtful if 100-percent eradication of the western pine beetle was accomplished in any of these experiments. Therefore deductions concerning flight distances that were predicated on the assumption of 100-percent elimination of beetle populations on the experimental areas, are hazardous at best.

Observations of Migrations and Population Movements

As a general rule, the locations of infested trees from one generation to the next suggest a certain amount of population movement from place to place during the year. One year a tree or a group of trees is attacked on one 40-acre tract; later in the season, or the next year, a similar concentration and attack may occur on the same 40 acres, on an adjacent area, or as far as half a mile way. Yet under these conditions the beetles move in no constant direction nor do population centers shift in a fixed pattern. The beetles appear to be just milling around in the infested areas.

At times, however, what appears to have been mass movement of western pine beetle populations has been observed. Records indicate that these beetles traveled in numbers for fairly long distances and in a fixed direction. Such movements have been observed but rarely, and then when great centers of population have built up to the point where favorable host material was becoming exhausted.

Miller (*93*) found in 1922 that after heavy populations of western pine beetle built up in wind-thrown material, new centers of western pine beetle attack suddenly appeared in areas where there had previously been little infestation. He reported: "Although the heaviest killings were found close to the largest bodies of wind-thrown trees, groups of beetle-killed trees were found at points from 6 to 8 miles distant from any mass of windfalls. Apparently this was the result of a flight of part of the beetles emerging from the down logs."

The sudden appearance of large groups of newly attacked trees in areas where previous infestation had been negligible has also been observed during epidemics. One unreported case is that of the

Fence Meadow epidemic on the Sierra National Forest. An epidemic killed a high percent of the pine in the marginal sites of Blue Canyon from 1929 to 1931. The infestation in this area declined in 1932, but late in the summer of that year large groups of ponderosa pine were attacked in the adjoining Fence Meadow area—2 to 4 miles from the Blue Canyon infestation and on good sites from 1,000 to 2,000 feet higher in elevation. Since there had previously been no noticeable infestation where these new attacks occurred, the shifting of epidemic centers gave the impression of a mass movement of beetle populations.

Gustafson (*U76*) attributed losses in a reserve stand on the Sierra National Forest to the migration of beetles from heavy infestation centers several miles away: "The 1931 summer infestation was characterized by a tendency on the part of the beetles to leave the lower yellow pine belt, where the preceding winter attacks had localized, and strike in Site I and II conditions at the higher elevations. This apparent migration invaded the sale area, causing the loss of many seed trees left after cutting."

The available evidence is not conclusive, but it suggests that the western pine beetle may occasionally migrate in numbers for long distances; also, that the migration occurs only under exceptional conditions, where large populations have developed to the point of overcrowding.

Summary of Information on Flight Behavior

1. At the beginning of their flight period, western pine beetle adults are positively phototropic to the extent that they will move toward lighted and away from darkened areas. However, the source of light appears to be only one of a number of factors that determine their direction of flight in the forest.

2. The beetles have been observed in flight only during daylight hours. There are no records of beetles coming to artificial lights at night in forest areas.

3. Optimum temperatures for flight activity appear to be between 70° and 85° F. The beetles do not maintain flight when temperatures approach 50° and below, nor when they are above 95°.

4. The beetles have not been observed to fly in swarms, that is, large numbers of beetles moving en masse.

5. The beetles have been observed to move both with and against air currents. The extent to which wind movements may influence direction of flight has not been definitely determined, but dispersion of broods does not seem to be dependent upon prevailing wind movement.

6. Flight distances traveled to attack trees vary anywhere from the immediate vicinity of the emergence up to 2 miles or more.

7. There is some evidence that under special conditions populations may migrate for distances as great as 6 to 8 miles.

8. On the whole, the original conclusion of Webb (*144*) that "they may select trees close at hand or may fly for quite a long distance before making a selection" has not been modified by years of subsequent studies of flight habits.

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THE SEASONAL GENERATIONS

Definitions

Hopkins (*44*) interpreted the term "brood" to mean "the progeny of a single pair (of beetles), or the individuals hatching from the eggs in a single egg gallery." The term "generation" he interpreted to mean all of the broods that are the offspring from eggs deposited at about the same time. True biological generations would be all the progeny of the same genealogical rank, but these are impossible to follow in the field because parent adults lay some eggs in the fall and then, after overwintering, may lay a second or third set of eggs in one or more trees in the spring.

Hopkins recognized the difficulty of distinguishing generations although he did not mention the complication due to the re-emergence of parent adults.

> All the progeny of the overwintered broods may be said to comprise a complete generation. If all of this progeny complete their development between the time the first eggs are deposited in the spring and the close of the same season of activity, and emerge from the trees, it may be referred to as constituting a complete seasonal generation. If another set of broods develops to maturity from eggs deposited by the adults of the first generation of the season, it will form a complete second generation, and so on. If, however, only parts of the broods complete their development and emerge during the first season, and the others remain over until the next season, it will be a partial development of a seasonal generation. If all of the broods develop and emerge within twelve months from the time the first eggs were deposited, it is referred to as a complete annual generation.

In attempting to follow Hopkins' definitions, fieldworkers have found it most convenient to separate the seasonal generations by trees infested by beetles at any one period rather than by true biological generations. The first trees that are attacked in the spring by the emerging overwintering broods are known as *first generation* trees. When adults develop and emerge from these first generation trees, the new trees that they attack are known as *second generation trees.* If broods develop and emerge from second generation trees and attack before winter, these are the *third generation trees*, and so on. For the trees attacked by the main emergence of adults developing from advanced overwintering larvae, this classification corresponds to the true generations because the broods all pupate and the beetles emerge at about the same time owing to the temperature bar to prepupal development.

But the classification of trees according to true generations becomes very complicated as the season advances. Trees of the second generation may be attacked by new adults emerging from first generation trees, by late adults emerging from overwintering trees, and by emerging parent adults. By the close of the season the overlapping of broods, together with differences in rate of development due to temperature, exposures, sites, and elevations, make the recognition of trees according to true generations practically impossible. Consequently a simplification in the terms used to designate the trees by seasonal generations has come into general use. The trees killed

each year are separated only as *overwintering trees*, in which broods carry through the winter, and as *summer generation trees*, which are attacked and abandoned by the beetles within the season of activity.

Significance of Generations

Studies to determine the number of generations have had two broad objectives. One was to obtain information useful in control. For this purpose it was desirable to determine the time of year that control work can be undertaken with assurance of finding all of the broods in the host trees. The second objective was to determine the destructive potential of the beetle. At least in theory, two generations annually should kill twice as many trees as one generation.

Seasonal Generations by Subregions

Records from infested trees have provided the basis for determining the number of seasonal generations that develop in any particular locality or subregion. Such records are available from six localities that represent fairly well the climatic and other variables that affect development of the beetle throughout most of its geographical distribution. It can be assumed from these studies only that the seasonal generations which were recognized represent the individual interpretation of each observer. The principal events that determine the number of generations are date of emergence of overwintered adults, the first attack in the spring, the rate of development in these first attacked trees, the subsequent emergence, attack, and development on successive groups of trees.

Princeton, British Columbia

(Lat. 49½° N., long. 120½° W., elev. 1,200–2,500 ft.)

Swaine (*131*) studied an outbreak of the western pine beetle in this northern limit of the ponderosa pine belt, and reported one brood and a partial second each season.

Southern Idaho (Centerville Area)

(Lat. 44° N., long. 116° W., elev. 3,000 ft.)

Webb (*144*) studied the life history of the beetle in southern Idaho in 1905 and recognized one and a partial second generation each season. The *first seasonal generation* attacked trees the latter part of June and emerged the latter part of August. Webb stated: ". . . the majority of (these) broods develop and emerge by the first part of September . . . but . . . some may continue to develop and emerge until in October; . . . possibly some pupae and young and matured adults may hibernate along with the larvae."

The *partial second generation* made its attack in late August and early September and these broods carried into the winter in the larval stage. "Eggs . . . were found August 26 and as late as September 13 . . . Thus it appears that the second generation . . . passes the winter in the larval stage and develops and emerges by the middle of the following June to the first part of July."

By interpretation of the life history in southern Idaho, Webb forecast the number of seasonal generations to be expected in the warmer localities: "It is probable . . . that at more southern and warmer localities in the Pacific Coast region there would be two complete generations and possibly a partial third." This surmise has been found to be approximately correct by subsequent studies.

East Central Oregon (Ochoco Area)

(Lat. 44½° N., long. 120½° W., elev. 3,500–5,000 ft.)

Buckhorn (*U39*) followed the seasonal generations in central Oregon from 1932 to 1935. He found considerable difficulty in separating the generations in the attacked trees. For example, in 1934 he found one set of trees attacked April 14 to 17 by re-emerging overwintering parent adults, and a month later (May 20) by the first emergence of overwintering new adults. Then a second series of trees was attacked by adults from overwintering larvae. The emergence from these two series of first generation trees occurred the last half of July and throughout August.

The main seasonal generations recognized by Buckhorn (*U39*) in this locality included:

First seasonal generation.—Attack by this generation occurred through the latter part of May and extended to the first of July. The emergence from these trees occurred in late August and extended through September. In trees of this generation he found that "a few individuals remained in the bark to overwinter as mature or prepupal larvae."

A partial second generation.—Attacks of this generation occurred the latter part of August and through September. Buckhorn estimated that from 10 to 45 percent of this generation emerged from the south side of trees during September and October. The remainder overwintered as two-thirds-grown to full-grown larvae.

A partial third generation.—Attacks occurred in late September and October and broods from these went into the overwintering stage as eggs to half-grown larvae. Buckhorn considered that these third generation trees were attacked by a combination of late emerging adults from first generation trees, plus early emergence from second generation trees. The emergence of beetles developing from this generation, except for the re-emergence of parent adults in the early spring, did not occur until the following May and June.

Southern Oregon (Rogue River Area)

(Lat. 42½° N., long. 123° W., elev. 3,000–4,000 ft.)

The life history of the beetle was studied intensively near Ashland, Oreg., by Keen (*U130*) in 1915 and 1916. He found that the attacks in some *first generation trees* occurred as early as March 4, as a result of emergence of overwintering new adults and emergence of parent adults; however, the peak of the attack by adults from overwintering larval broods did not reach a maximum until June 22. Emergence from these first generation trees occurred during the latter part of July and through August.

The attack of *a partial second seasonal generation* began the first of August and reached its maximum September 6. A few new adults of this generation completed their development and emerged before winter; the remainder of the broods overwintered as full-grown larvae and emerged the following spring.

A *partial third generation* developed from attacks occurring in September and October. Broods developing from these attacks overwintered as eggs and small larvae, and did not emerge as new adults until the following June.

In summing up the seasonal activity, Keen (*U130*) stated:

> There are 3 periods of attack, 3 of egg laying, 3 of larvae hatching, 3 of pupation, 3 of beetles forming and 3 of emerging. These periods overlap to some extent, upon beginning and ending, but their points of maximum activity are easily distinguishable. Neither are they of equal magnitude. The overwintering generation is the largest generation; the first seasonal generation somewhat smaller, and the third partial generation very small indeed. . . . There is in general one annual (seasonal) generation with a partial second and a partial third. At Ashland, Oregon, there is a maximum of 2 (complete) annual generations and a partial third, and a minimum of 1 annual generation.

Northeastern California (Modoc Area)

(Lat. 41½° N., long. 121° W., elev. 5,000 ft.)

Studies were made near Hackamore, Calif., by Furniss (*U68*) in 1933. He was able to distinguish the following seasonal generations for this locality (fig. 13):

A *first seasonal generation* was established between the first of June and the first of August. Emergence occurred from the first of August to the middle of September.

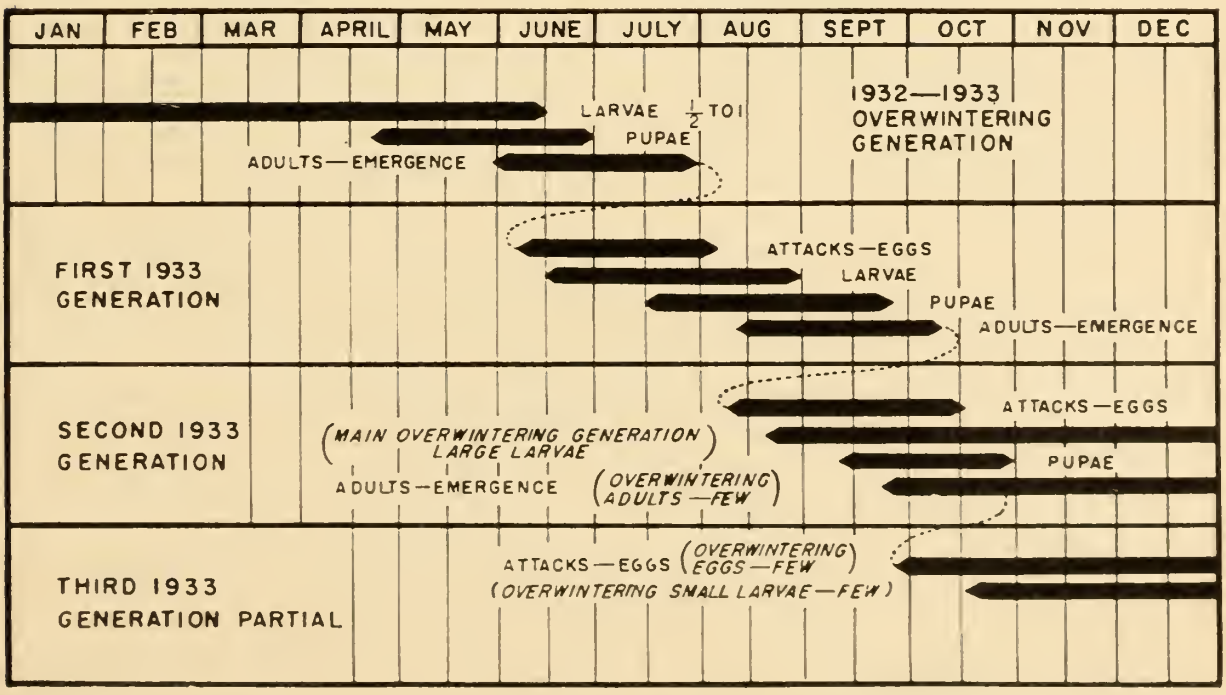

FIGURE 13.—1933 seasonal generation of the western pine beetle, Hackamore, Modoc National Forest, Calif.

A *partial second seasonal generation* was established from the first of August to the middle of October; a partial emergence began near the middle of November. By far the greater part of this generation overwintered in the large larval stage.

A *partial third generation* was established during October and the first part of November. The broods passed through the winter in the parent adult, egg, and very young larval stages, and were estimated to represent about 10 percent of the overwintering population.

Southern Sierra Region (North Fork Area)

(Lat. 37¼° N., long. 119½° W., elev. 3,000–4,000 ft.)

Seasonal history studies were carried on at Bass Lake, near North Fork, Calif., in 1926 and 1927 by Person (*U238*); in 1932 by Furniss (*U64*), and in 1933 by Salman (*U270*). Considerable variation was found between years, and it is not certain that all three workers agreed entirely as to their interpretations of generations. Nevertheless, their records show at least three seasonal generations in this southern range of the beetle's distribution (fig. 14). In general, the following seasonal generations were recognized:

A first seasonal generation.—Attacks were recorded from April 25 to the latter part of May, the peak usually coming around the middle of May. Emergence from trees attacked by this generation began soon after the middle of June and extended to the first of August, the peak of emergence occurring during the first half of July.

A second seasonal generation.—Attacks of this generation occurred from the last of June to the middle of August. Emergence began during the first half of August and extended to the end of September. The peak of emergence of this generation occurred during the first part of September.

A partial third seasonal generation.—Attacks of this generation occurred from August 15 to November 1. This generation overwintered mostly in the large larval stage. In the earliest of these third generation trees, the brood completed development and emerged during October and November. In those trees attacked late in the season, the broods went into the overwintering stage as parent adults, eggs, and small larvae.

A fourth seasonal generation was recognized by Furniss in 1932 season and by Salman in 1934. The attack was established in the late fall (November) by a small part of the third generation which emerged in October and November. This generation overwintered in the parent adult, egg, and very small larval stages.

Differences in Development of Seasonal Generations

Rate of development responded to temperatures with fair consistency in several studies. Therefore the number of generations produced in a season should be easily determined from the cumulative hour-degree temperatures above the zero of development for any given locality. But those who have studied temperature re-

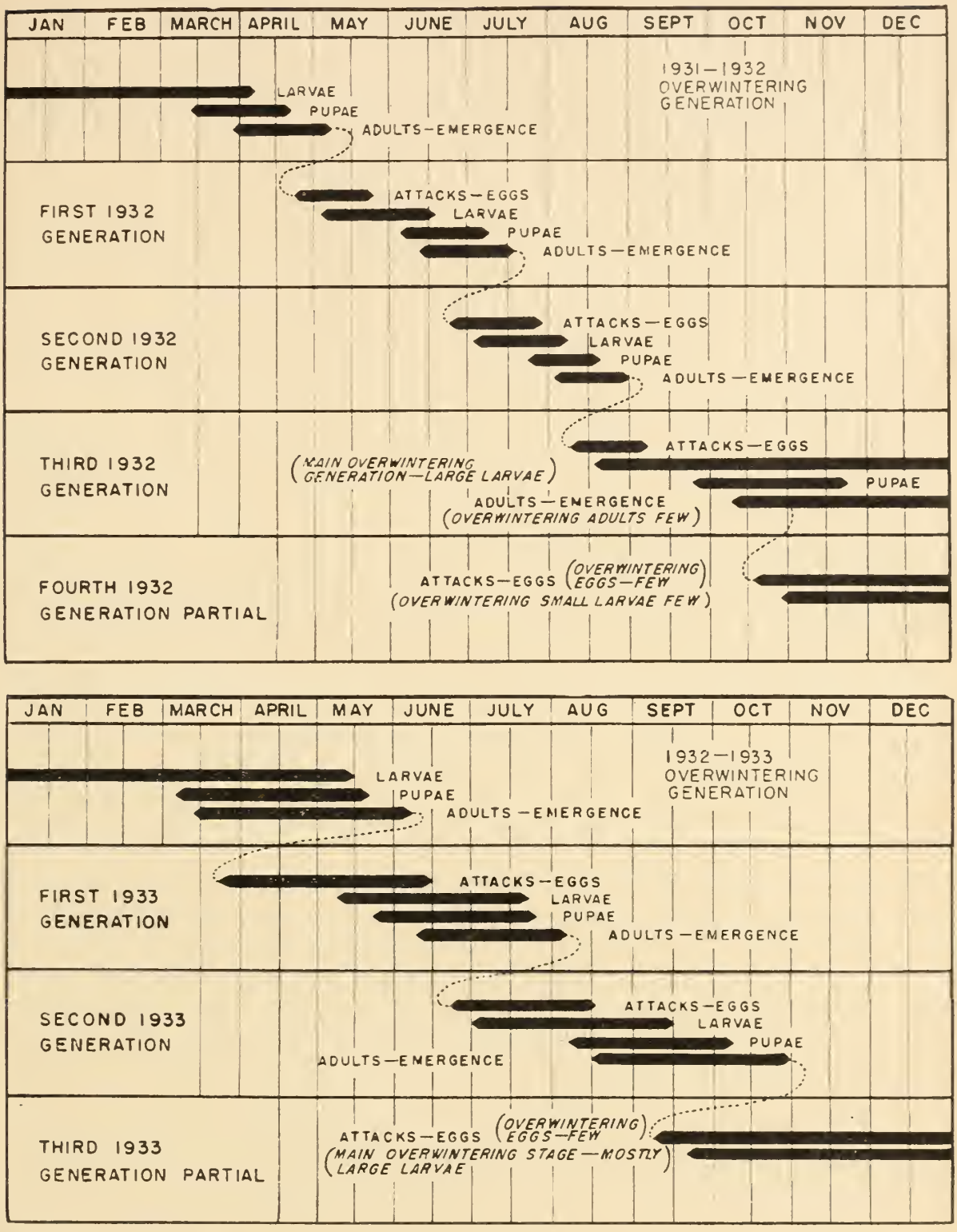

FIGURE 14.—Comparison of the 1932 and 1933 seasonal history of the western pine beetle in the southern Sierra subregion of California.

quirements have not found the determination so simple. Whiteside (*U331*), after carrying through a long series of experiments on the development of mature larvae to callow adults, concluded: "There appears to be no temperature which may be called the zero of development that will cover all stages of the western pine beetle at different seasons of the year."

Factors that appear to be important in modifying the number of seasonal generations are latitude, longitude, altitude, exposure, and climatic differences between areas and seasons.

Differences by Latitude and Altitude

In discussing the general seasonal history of the genus *Dendroctonus*, Hopkins (*44, p. 19*) allows for the modification of seasonal development by latitude and altitude, in accordance with his bioclimatic law:

> In the spring of a given year the average difference in the time of beginning activity, emergence, flight, attack, etc., at the same altitude, will not vary much from four days later for each degree north, or four days earlier for each degree south, while at the same latitude there will be a difference of about four days for each 400 feet difference in altitude—four days later for each 400 feet higher, and four days earlier for each 400 feet lower.
>
> In the fall of the year the beginning of hibernation and other events will be earlier northward and later southward at localities of the same elevation, or earlier at higher altitudes and later at lower altitudes in the same latitude.
>
> Of course there are exceptions to these rules, especially in regions like that of California, where remarkably abnormal conditions as to influence of altitude and latitude prevail, as also in the case of southern and northern exposures, sandy dry soils, and wet clayey soils or bogs.

Differences by Subregions

The differences in seasonal generations by subregions can be accounted for largely by difference in latitude and longitude. According to Hopkins' (*44*) bioclimatic law, there should be a difference of about 30 days in the occurrence of any given biological event between central Idaho and the southern Sierra Nevada at the same elevation. Actually, the observations indicate a difference of about 60 days in the dates of attack by the first seasonal generation in the spring, and nearly the same difference in close of activity in the fall. The British Columbia record indicates as short a season as that in Idaho. The central and southern Oregon and the northern California conditions represent about the median of the range in time of given brood activities. Here the normal brood development takes place in one complete seasonal generation, a second partial generation, and a third partial generation each year.

Differences by Elevation

The influence of elevation, according to Hopkins' bioclimatic law, is to retard development 1 day for each 100-foot rise in elevation. However, this rate seems to be nearly doubled in western mountain areas, and is greatly modified by such topographic features as slope and exposure.

In November 1915 workers at Ashland, Oreg., removed slabs of bark from a tree heavily infested with the western pine beetle and placed pieces of bark about 2 feet square on the north side of trees at a series of nearby altitude stations running from 2,700 to 5,700 feet. During the spring of 1916 these stations were visited at weekly intervals and emergence records taken.

Hopkins (*45*) reported the results of this experiment in the form of a table showing the departures from his bioclimatic-law rates (table 1). Hopkins commented that this table "shows a striking example of departures from the constant caused by local influences."

TABLE 1.—*Effect of altitude on emergence of the western pine beetle*

Altitude (feet m.s.l.)	Departure from base station		
	Computed	Actual	Difference
	Days	*Days*	*Days*
5,700	−25	+53	+28
5,200	−20	+36	+16
4,600	+14	+26	+12
4,200	+10	+19	+9
3,700	−5	+3	−2
3,200 [1]	0	0	0
2,700	−5	−17	−12

[1] Base.

In 1917 Miller attempted to determine the effect of elevation in the same locality and season by cage control on trap logs. He found that at the 2,000-foot elevation, two seasonal generations were completed between May 10 and October 15; at the 5,000-foot elevation, a few miles distant, only 1 partial generation was completed between the same dates.

Differences by Exposure

In the altitude experiment, some slabs of infested bark also were placed on both the north and south sides of the tree. Hopkins (*45*) reported a 20-day difference in the appearance of first pupae, a 35-day difference in transformation of first adults, and a 35-day difference in first emergence, the warmer south side always being earlier.

Differences by Seasons

Records show that the rapidity of brood development may differ markedly between seasons, depending upon temperatures and length of growing season (fig. 14). But at most the difference does not account for more than one extra partial generation. This seasonal difference is evident in a series of records from North Fork, Calif. (*U68, U270*). Here the seasons of 1926 and 1933 were considered to have produced 2 complete seasonal generations and a partial third; the seasons of 1932 and 1934 produced 2 complete seasonal generations, a partial third, and a partial fourth. Furniss (*U68*) attributed the difference to an early warm spring in 1932 and cold weather in the spring of 1933.

Effect of Re-Emerging Parent Adults on Generations

The re-emergence of parent adults and their extended period of egg laying in more than one tree complicates a determination of number of generations and their exact beginning and ending. Attacks

and egg laying by emerged parent adults often fill in the gaps between attacks by new adults. In 1934 the activities of the emerging parent adults were closely followed (*U270*). They were considered to have produced two secondary generations that overlapped the primary generations produced by the bulk of the broods (fig. 15).

Summary of Information on Generations

(1) True biological generations of the western pine beetle are subject to so much overlapping and confusion as the season advances that they are impossible to follow. Generations therefore are arbitrarily separated according to the time that infested trees are attacked and the period during which the bulk of beetle populations, regardless of origin or heredity, are found living in a given set of infested trees.

(2) Although temperatures and other climatic influences accelerate or retard development of the western pine beetle, the number of generations produced annually is limited by the climatic extremes within which the principal host tree, ponderosa pine, grows. This tree occurs naturally only where a definite winter period induces dormancy in tree growth, and development of broods of the beetle. Although minimum winter temperatures differ widely in the range of ponderosa pine, maximum summer temperatures and the length of season during which the beetles are active differ relatively little.

(3) The number of seasonal generations differs between subregions and localities and between seasons in the same locality. On the average, each season has three distinct periods of attack, egg laying, and brood development. The result is one complete seasonal generation, a partial second, and a partial third. This average may be modified by climatic extremes within the range of the beetle. The minimum is one complete generation and a partial second generation; the maximum, two complete generations and partial third and fourth generations.

(4) For purposes of control, the overwintering generation is the only one in which all of the broods may be found in the bark of infested host trees.

(5) The degree of loss sustained in any particular region or year seems to have little direct relation to the number of generations produced annually.

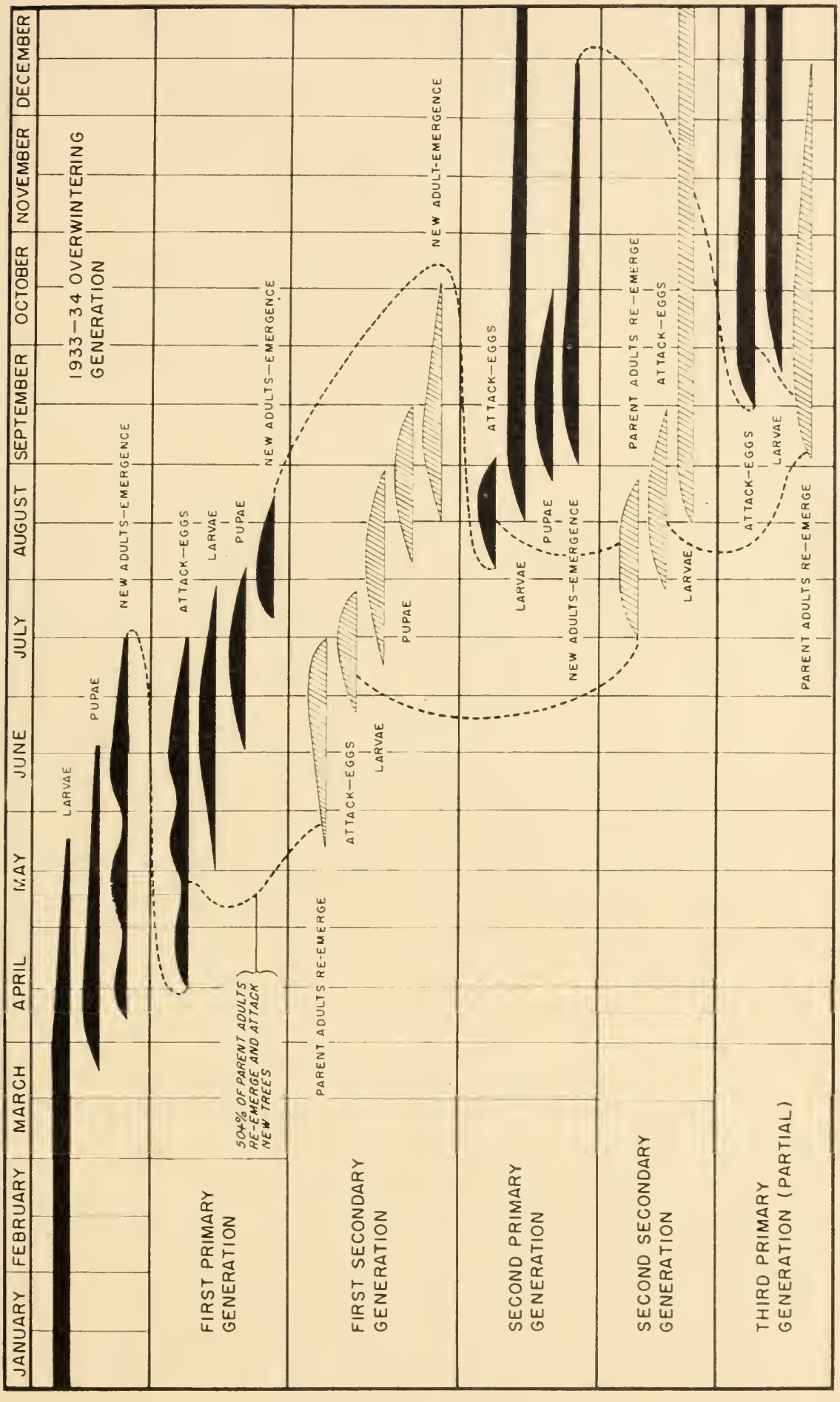

FIGURE 15.—Seasonal development of the western pine beetle, 1934, Modoc National Forest, Calif.

SECTION II. BIOTIC RELATIONSHIPS OF THE WESTERN PINE BEETLE

THE BIOTIC POTENTIAL

Population Potential

Knowing the egg laying capacity of the western pine beetle, one might easily find by computation that its potential progeny could be quite overwhelming in a very short time. With an average of 48 eggs per female and 2 generations a year, 1 pair of beetles could produce 48 adults after the first generation, of which 26 would be females and 22 males; and 1,248 adults after the second generation, of which 674 would be females and 574 males; and 32,352 adults after the third generation. With this rate of increase, the progeny would reach astronomical proportions after a few years.

If we disregard this potential and instead compare the number of beetles that attack a tree with the new adults that emerge, we find that on the average enough beetles are produced in 1 tree to attack and kill 5 more rees of the same dimensions; these in turn should produce enough beetles to kill 25 trees; and by the third generation, we can expect a loss of 125 trees. This may not seem like a high rate of increase compared with the capacity of other insects, but the tenth generation of progeny from beetles in the first tree would be capable of killing 9,765,625 trees. If unchecked, the population would soon kill all the ponderosa pine trees in the West.

We know that nothing of this sort ever happens. The long history of western pine beetle epidemics shows that population increases are inevitably followed by decreases. Somewhere in the complex environment of the beetle are factors that keep its numbers far below its potential. These natural factors of control have been the subject of much speculation and study since the beginning of bark beetle investigations.

Hopkins (*44*) considered that climatic influences, temperatures, trees injured by lightning and fires, slash from storms and timber cutting, and trees affected by overmaturity and diseases are all environmental factors that operate in some cases for and in others against the increase of bark beetle populations (*Dendroctonus* spp.). Among the direct enemies of the beetles, he mentioned predatory and parasitic insects, birds, and insect diseases. His discussion was too generalized to serve as a basis for recognition of specific conditions that forerun an increase or decrease of beetle populations. Since then many workers have tried to take apart the complicated biotic relationships of the western pine beetle and to find out by analysis just what the controlling factors are and how and when they operate.

Population Statistics

The first attempt to determine the number of beetles that make up the population of an infested tree was made by Riggs (*U250*) in 1913. He felled a tree 32 inches d.b.h. (diameter breast high, i.e.,

4.5 feet above ground) and 142 feet in height containing overwintering broods for 102 feet of infested length, cut up the bark, and counted all the brood he could find in the inner and outer bark. He reported finding a total of 33,230 larvae and young adults. No one ever attempted to verify or dispute his figures.

On the basis of the brood statistics determined from all the bark counting done so far, a fair estimate of the total population of an infested tree is as follows:

Item:	*Average per square foot*	*Per average tree*[1]
Number of parent adults attacking	25	8,625
Number of eggs	648	223,560
Number of larvae:		
Advanced larval period	188	64,860
Prepupal period	122	42,090
New adults emerging	92	31,740

[1] Based on average tree of 25.2 inches d.b.h., bark surface 345 square feet.

Normal Brood Mortality

As these average population statistics show, the potential increase in beetle population as determined by the egg laying capacity of the female is normally reduced in each stage of brood development. From 648 eggs laid per square foot by 25 parent adults, only 92 beetles developed, a reduction of 86 percent. Thus only about 1 egg out of 7 actually becomes an adult and finally emerges. What happens to the other six eggs is still unknown. Of the beetles that emerge, a great many are undoubtedly lost in flight and never manage to make a successful attack.

In addition to what might be considered as normal mortality, broods are frequently affected by some catastrophe, such as extreme cold weather, which produces abnormal or nearly complete mortality. Thus the vicissitudes of a beetle's existence and the many natural control factors operating to reduce its population are what save forests from early and total extinction.

FACTORS CAUSING BROOD MORTALITY DURING DEVELOPMENT IN THE HOST

During the long period of brood development in the bark of the host tree, the hazards of life are many, and at any stage from egg to adult mortality may occur from a variety of causes. The causes of mortality that have been explored include unfavorable moisture, lethal temperatures, nutrition, competition for food supply, parasites, and predators.

Unfavorable Moisture Conditions

Either excess moisture or extreme dryness of the bark may be unfavorable to brood development and cause mortality. Keen (*U130*) made the following observations on the effect of excessive moisture on the hatching eggs:

> No definite figures were obtained on the average percent of eggs hatching. However, it was noted that in some cases a good many eggs die or are killed in the egg niches. In some sour-sap trees,

the entire brood may be killed by the moist condition. In other trees, which are normal, a varying percent fail to hatch.

Excessive moisture conditions in the inner bark appear to be quite detrimental to the first instar larvae. The high mortality of young larvae in the inner bark of "sour-sap" trees has often been noted.

Beal (*U6*) measured the moisture content of logs and slash where high brood mortality was occurring and reported that:

> . . . excessive phloem moisture of 200 to 300 percent which invariably obtains in logs and slash kept within the temperature limits for brood development may be responsible either directly or indirectly for a large share of the brood mortality. We know that in standing trees where brood development of the western pine beetle proceeds normally, there is a rapid loss of moisture.

Whiteside (*U331*) undertook to determine the amount of moisture in the outer bark which permitted satisfactory brood development. He determined the moisture content in 12 bark samples from infested trees with normal development and found that this averaged 12 percent on an oven-dry basis. This condition in the outer bark corresponded to a relative atmospheric humidity of 56 percent.

The actual correlation between the amount of bark moisture and larval mortality is yet to be determined quantitatively. General observations indicate that excessive moisture conditions which produce high mortality occur at times in the field, but are only in sour-sap trees, slash, and windfalls. The sour-sap conditions usually occur only in the lower bole of standing infested trees; therefore broods in the upper bole are not affected.

The amount of desiccation necessary to produce mortality in bark has not been given attention. Rearing of exposed larvae in dry rooms has demonstrated that they can withstand considerable desiccation. It would appear that in nature the moisture stored in the sapwood of attacked trees and logs is passed on to the inner and outer bark in sufficient volume to provide for satisfactory brood development.

Lethal Low Temperatures

The western pine beetle, like all other forms of life, cannot survive extremes of either high or low temperatures. The early western pine beetle studies found that subzero weather of −15° to −20° F. usually results in some mortality among overwintering broods. If such temperatures are prolonged, or if the minimums fall much below −20°, the mortality may be high and populations of the beetle will be greatly reduced. The mortality of broods resulting from low temperatures has been thoroughly investigated. A long list of publications and reports deal with this subject. Hopkins (*44*) referred to the effects of low temperatures only briefly:

> While the severe cold at high elevations in which most of the western species prevail appears to have no detrimental effect on the overwintering broods, we have a striking example of its effect on a northern migration of a southern species in the complete extermination of the southern pine beetle in the Virginias by the exceptionally cold winter of 1902–03.

In December 1924 minimum temperatures of −20° to −25° F. occurred on the Metolius area, near Bend, Oreg., where a control

project was underway (*94*). After this cold spell, from 25 to 80 percent of the overwintering larval broods were dead in the bark.

The importance of low temperatures in the reduction of beetle populations was emphasized by extreme cold spells during the winter of 1932–33 in Washington, Oregon, and northern California. The first cold wave of early December 1932 brought temperatures of from −20° to −38° F., throughout the entire range of the beetle in the interior ponderosa pine type. A second cold spell in February 1933 dropped temperatures to an all-time low in Oregon of −54°. These cold periods resulted in brood mortalities ranging from 50 to 90 percent. The average mortality throughout the eastside pine type of California and Oregon was estimated at 70 percent. The effects of this freeze upon the 1933 beetle population were closely studied through the funds and facilities made available by the Civilian Conservation Corps program of the Forest Service (*96*, *97*, *98*).

Other periods of cold weather which resulted in some reduction of populations were recorded in November 1935, in January 1937 (*U274*), and in February 1939 (*U327*). Appreciable mortality from these cold spells, however, was found only in local areas. No other cold periods have been recorded that were as severe as the historic cold wave of December 1932 in causing beetle population reduction.

The potentialities of cold weather as a factor in the natural control of the beetle were considered to warrant intensive investigations in the field and in the laboratory. Studies by entomologists of the western forest insect laboratories were initiated in 1933 and continued until 1940. The results of this research program have provided an adequate basis for the interpretation of lethal temperatures in the natural control of the beetle.

Laboratory Studies

Hundreds of laboratory tests were made to determine what happens to the larvae when they are exposed to temperatures below the range in which they are able to maintain activity. Most of these studies have been concerned with temperatures below freezing. Sometimes infested bark was exposed to the temperatures under study and results were determined by shaving up the bark and recovering the larvae. In other experiments, entire blocks or small logs were exposed. In the greater number of tests, however, mature larvae were exposed "naked" to cold air in refrigeration compartments.

The study technique that was most generally adopted after various trials with different media and procedures was described by Miller and Struble (*U208*). Larvae were removed from bark and placed in an individual paraffin cell. These cells were in blocks of 50 each and were open at the top so as to permit free access of air to the body of the larvae; at the same time the paraffin walls protected the larvae from each other and from the hazards of handling. An important requirement was an allowance for sufficient time of exposure at any given temperature for the body of the larvae to be chilled to that point.

When the larvae were exposed to a gradual lowering of air temperatures at a rate of 4° or 5° F. per hour, the effects of any given temperature became apparent very soon after the point was reached. Larvae that were transferred suddenly from warm temperatures to

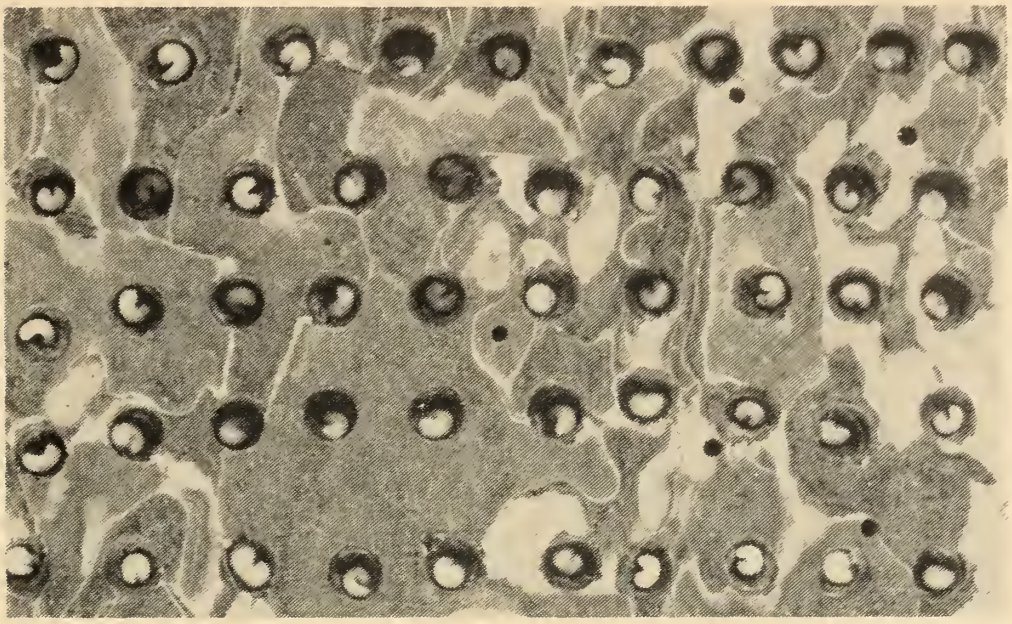

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FIGURE 16.—Cells in ponderosa pine bark used in exposing larvae to critical low temperatures.

temperature held at any fixed point below freezing required about 2 hours for the effects to register. In general, the containers, whether natural bark (fig. 16), paraffin cells, or paper cells, made little difference in the results as long as the body of the larva was chilled to the temperature under consideration.

Terms Used in Defining the Effects of Temperatures

If many western pine beetle larvae are exposed under perfectly uniform conditions to the same range of air temperatures from 0° to −10° F., they will not all die at the same time or at the same temperature. For overwintering broods it has been found, on the average, that after larvae have been chilled to a temperature of 0° F. the mortality will vary from 20 to 50 percent; at −2½°, from 50 to 75 percent; at −5°, from 75 to 100 percent; but at −7½° the mortality is nearly always 100 percent. These differences in the amount of mortality, due to individual variations in cold resistance among any selected group of larvae at given temperatures, have made it necessary to adopt terms applying to these variations. The following were proposed by Miller and Struble (*U208*) and have been generally used in subsequent studies.

Temperature points.—The minimum temperature to which the body of the insect is chilled.

Freezing point.—The temperature at which the body of the insect becomes frozen owing to crystallization of the free water in the alimentary canal and body tissues; this condition does not necessarily result in death. The term was first used by Robinson (*114*).

Critical point.—The temperature at which death occurs as a result of cold. The bound water crystallizes and the body cells are destroyed. This point may occur from 5° to 10° below the freezing point.

Critical range.—The range of temperatures from the highest point where some mortality due to cold occurs to the lowest point where complete mortality occurs. The *initial critical point* is the highest

temperature in the critical range; the *ultimate critical point* is the temperature at which mortality becomes complete; and the *intermediate critical points* apply to temperatures within the critical range.

Low Temperatures That Affect Larvae

Low temperature effects are best discussed by proceeding from those at higher temperatures to those at lower temperatures in the range that has been studied.

50° F.—Larvae at this point and below become sluggish and dormant. "Failure of broods to develop at low temperatures below 50° F." (*U6*) indicates that metabolism ceases.

15° to 10° F.—Larvae may "freeze," but recover if brought back to warm temperatures (*95*). Recovery is apparently dependent on the amount of free water in the tissues. Yuill (*U340*) was unable to develop this condition by exposing larvae at 12° to 14° and stated that "in these tests, the larvae did not freeze until exposed to a temperature of 10° F. or less and the effects in practically every case were fatal."

10° to 7½° F.—The initial critical points for active summer brood larvae occur here. Yuill (*U342*) found mortalities around 50 percent at 7½°. For overwintering larvae, no appreciable mortality due to cold occurred from exposure at 10° for 39 hours (*U208*). Yuill obtained low mortality (16 percent) of overwintered larvae after exposure of 4 days at 7½°.

7½° to 5° F.—These are highly critical points for active summer brood larvae. Yuill (*U342*) found 96-percent mortality for larvae of summer broods from the southern Sierra region, and 60 percent from the Modoc region, after 2 hours exposure at 5°.

5° to 2½° F.—Only a summer brood larvae survive these temperatures after 2 hours exposure. Yuill (*U342*, *U343*) found 100-percent mortality at 2½° for broods from the southern Sierra, and 84 percent from the Modoc. The initial critical points for the least hardy overwintering larvae occur within this range. Low mortality develops at 5°. Miller and Struble (*U208*) recorded 42-percent mortality after 1 hour of exposure at 2½°; mortality increased progressively with time of exposure up to 7 hours, when it reached 76 percent.

2½° to 0° F.—These are important critical points in which the first effective mortality of overwintering larvae becomes apparent. In many laboratory tests with overwintering larvae, mortality of 20 to 50 percent has always developed in this range. Miller and Struble (*U208*) compared overwintering broods from the Sierra, Modoc, Ochoco, and Coeur d'Alene areas, representing regional extremes in the range of the beetle, and found appreciable mortality at 2½° in all cases.

–2½° F.—This point is near the middle of the critical range for overwintering larvae. Mortality is variable, depending upon degree of conditioning, but is usually more than 50 percent.

–5° F.—High mortality of overwintering broods always occurs at this point. Two tests by Yuill (*U342*) show mortalities of 96 and 100 percent after 2 hours exposure.

–7½° F.—Larvae die quickly at this point, the mortality usually reaching 100 percent with an exposure of 1 or 2 hours (*U342*).

Only two records are found of survival at this temperature by conditioned overwintering larvae. Miller and Struble (*U208*) exposed broods in bark sections from Coeur d'Alene and Ochoco National Forests by gradually chilling the bark down to this point. The mortality in the Coeur d'Alene brood was 81.9 percent and that in the Ochoco material 75.7 percent. In a brood from Sierra National Forest, the mortality under identical treatment was 100 percent. In larvae removed from the bark and exposed in paraffin cells, the mortality at −7½° was 100 percent from all regions.

−10° F.—There is only one record of survival at this point in laboratory tests. Ten percent of the larvae in bark from Coeur d'Alene survived after temperatures had dropped to this point. Survival may have been due to variations in temperatures within the bark or to irregularities in temperature control.

−12½° F.—No larvae have survived exposure at this point in laboratory tests. In the field, however, using bulb thermometers under the bark, Beal (*U10*) found survival of 36 percent after bark temperatures had reached −14°; at −17° survival was 27.6 percent. This difference was thought to be due to one of, or a combination of these factors: First, the difference may be due to variation between field and laboratory tests. Second, temperatures in the field reached their low point for only a very brief period. Third, it may be that a previous freeze had already killed about 50 percent of the broods, and the remaining larvae may have been principally the hardier individuals. Fourth, broods from eastern Oregon probably are more cold resistant than those from the southern Sierra of California.

An example of the effect of the entire range of critical temperatures upon winter brood larvae is shown in figure 17. In this test larvae were exposed to temperatures gradually lowered from 10° to 7½° F. The experiment was carried out with controlled refrigeration and with larvae from Modoc National Forest in northern California exposed in paraffin containers (*U208*). Through the critical range, the temperature dropped at a rate of slightly more than 2° per hour. One lot of 50 larvae was removed when 10° was reached; other lots of 50 larvae each were removed at 5°, 2½°, 0°, −2½°, −5°, and −7½°. The mortality in each lot was determined 24 hours after removal. Mortality was 28 percent at 2½°; 34 percent at −2½°, and 100 percent at −7½°. Results of this test show that after chilling, brief exposures are critical to overwintering larvae at temperatures from +2½° to −2½° and that temperatures of −5° and below are fatal to most larval broods.

Cold Hardiness of the Larvae

In summarizing the work on cold hardiness of the western pine beetle, Yuill (*151*) recognized a summer and winter condition of the larval broods. "Under the summer condition, the critical temperature range was 10° F. to −2½° F.; and under the winter condition, 5° F. to −7½° F."

Yuill concluded that increased cold hardiness of the overwintering larval broods does not set in until late in the fall.

The critical range (10° to −2½° F.) remains at the same level with the beginning of cool weather late in October or early

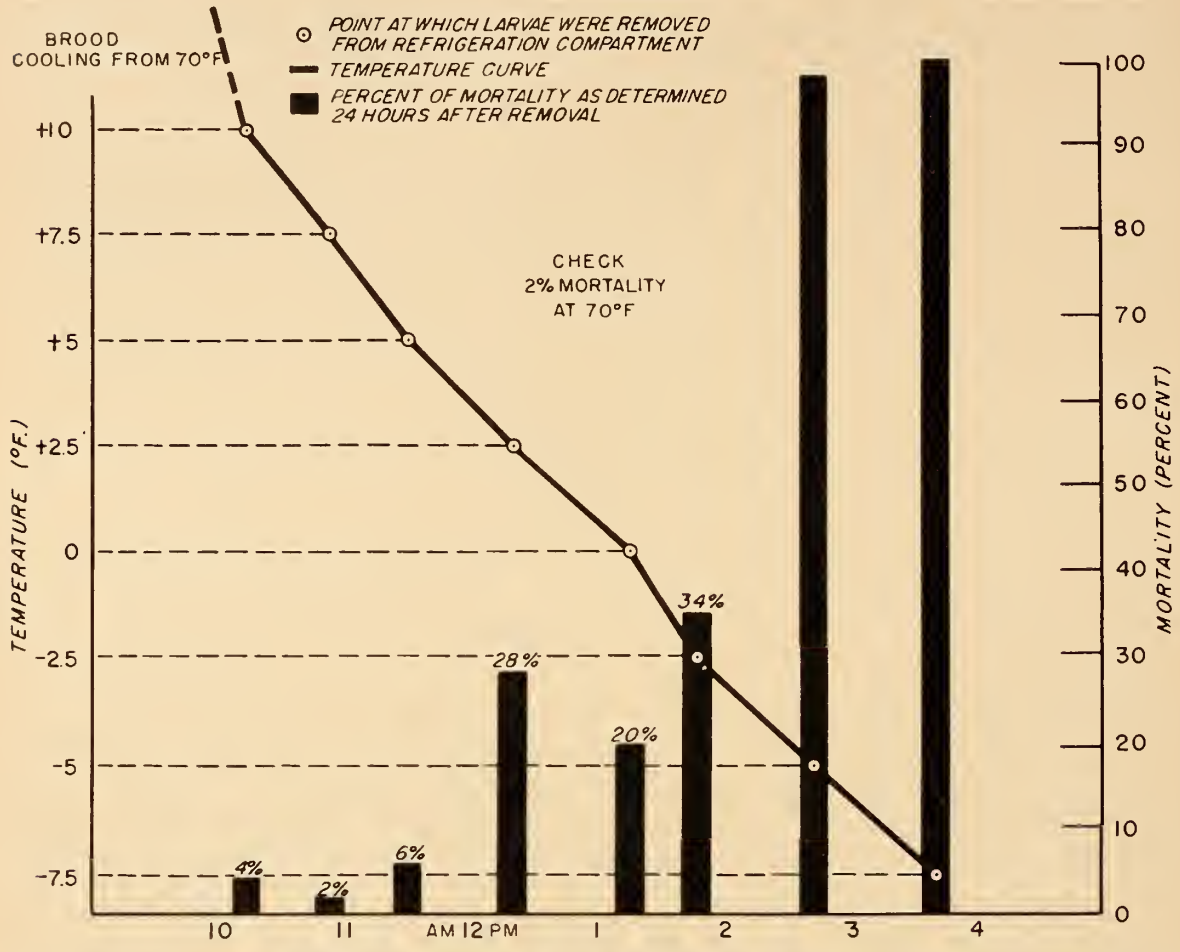

FIGURE 17.—Mortality of western pine beetle larvae when exposed in the laboratory to low temperatures (Feb. 13, 1934).

November, when within 6 weeks or less cold hardiness increases to the winter condition (0° F. to −7½° F.).—It also appears that the level of resistance developed each winter is always the same whether the season is mild or severe.

The degree of cold hardiness developed by the western pine beetle was found to be far less than that of its near relative the mountain pine beetle (*Dendroctonus monticolae*) in sugar pine. Although the difference in the critical range between summer and winter conditions of the western pine beetle was about 5° F., that of the mountain pine beetle was about 10°. According to Evenden (*U60*), the mountain pine beetle has been found to develop resistance to temperatures of −25° and −30° in lodgepole pine of the northern Rocky Mountain region.

Cold hardiness has been attributed to the ability of larvae to change the fat and moisture content of their bodies so as to prevent crystallization of bound water in the cells. Yuill (*151*) was able to induce a limited degree of cold hardiness by subjecting larvae for a long period to temperatures slightly above freezing. Larvae collected from the outer bark in November and stored at a temperature of 36° F. for a period of 35 days were able to withstand about 2½ degrees lower temperature than when first collected. Mountain pine beetle larvae survived temperatures 10° lower after similar conditioning.

A start was made by Yuill (*U344*) in determining changes in fat and moisture conditions that go with conditioning for cold hardiness

in both the western pine and mountain pine beetles. The results were little more than indicative.

> Although *D. brevicomis* larvae contained a much higher percentage of fats than do *D. monticolae* larvae, the iodine and saponification values were both lower than in the fat from the latter species. Such a fat would be less available under low temperatures and so might be a factor in limiting the development and resistance of this less hardy species.

Since studies of this type required a complicated technique and could be expected to shed light only on the fundamental phases of cold hardiness, they were not continued.

The Time Factor in Exposure to Critical Temperatures

Subzero temperatures to which overwintering larvae are exposed in the field usually last no more than a few days at the most. A number of laboratory tests were made to determine the importance of time in increasing mortality. Under refrigeration control, the lower critical temperatures required about 20 minutes' exposure to register the first lethal effects. After 2 hours of exposure, however, most of the mortality resulting from low lethal temperatures was complete. At the higher critical temperatures, mortality developed more slowly. These experiments were summarized and published by Yuill (*151*).

> When larvae are subjected to a temperature of 0° F., within the upper critical range, . . . the death rate increased rapidly up to two hours, and then continued to rise more gradually up to the seventh or eighth day. . . . Prolonged exposure at 0° F. had a pronounced effect upon the subsequent development of the survivors, for none of the larvae that were alive after an exposure of 6 days or more were able to reach the pupal stage when returned to developmental temperatures. (Fig. 18.)
>
> At −7½° F. practically all individuals were killed by exposures of 1 or 2 hours.
>
> In general then, it seems that for western pine beetle larvae the length of time they are subjected to lethal temperatures influences mortality only at points in the upper critical range; and at all other points the intensity of the cold, rather than the period of exposure, is the governing factor.

Critical Low Temperature for Eggs, Pupae, and Adults

Beal (*U6*) found that eggs did not incubate when kept at temperatures below 50° F. Miller (*U197, 95*) found that high mortality occurs when eggs are exposed to temperatures below 0°; only 50 percent of the eggs incubated after short exposure to a temperature of −5°; 90.7 percent of those exposed to −10° failed to incubate. In general, eggs respond to the same developmental temperatures as the larvae, and are killed by the same lethal temperatures.

Miller (*U197, 95*) reported that "pupae are somewhat less resistant to cold than larvae, as mortality was practically complete at −5° F." Later, however, Miller and Struble (*U208*) conducted parallel tests of larvae and pupae under identical conditions of exposure and

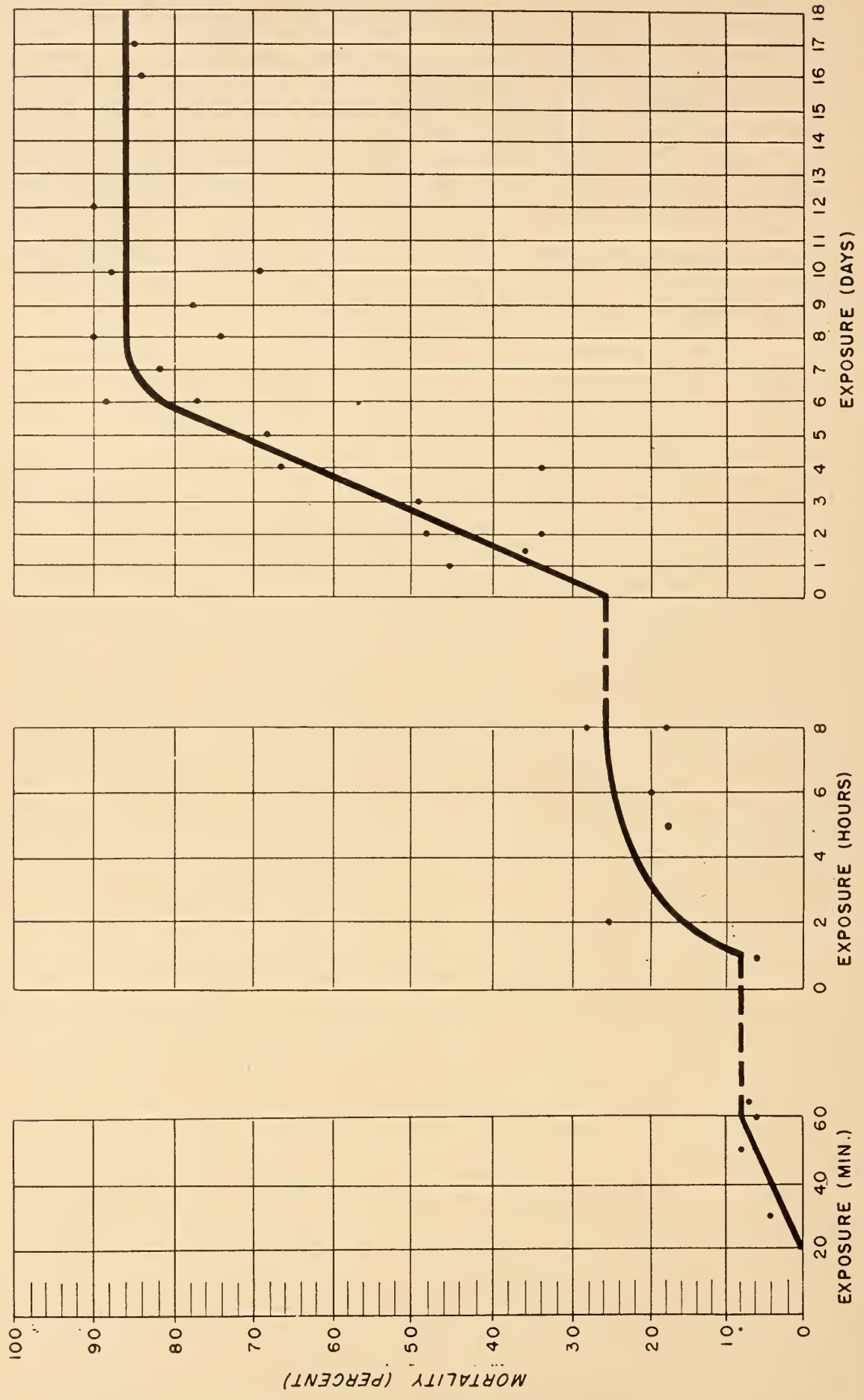

FIGURE 18.—Mortality of western pine beetle larvae under constant exposure to a temperature of 0° F.

found no difference in cold resistance between these two stages. "The range of critical temperatures and the ultimate killing points are essentially the same."

Miller and Struble (*U208*) checked the critical range for adults by testing 754 mature adults. Mortality first appeared at 14° F. and was complete at 10°. They had difficulties in determining whether adults shocked by cold were still alive:

> The actual mortality was very difficult to determine, many of the beetles exposed to temperatures at 12° and 14° F. being moribund for long periods and showing barely perceptible movement (of legs and antennae). However, the recovery of the beetles from exposure to 15° F. was quite definite as all became active in one-half hour when they were returned to warm temperatures. Also complete mortality at 10° F. was quite positive. Adults suddenly exposed to this temperature died with wings spread as though they had tried to fly before becoming thoroughly chilled.

Field Conditions Modifying Low-Temperature Effects

Relation of Air and Bark Temperatures

Early investigators recognized that bark could insulate larvae in infested trees and protect the broods when surrounding air reached lethal temperatures. Near Coeur d'Alene, Idaho, in December 1926, mercury bulb thermometers were imbedded in the bark on the north and south sides of infested trees during subzero weather. Thermometers were also suspended in the air next to the bark. Rust (*U251*) reported "When air temperatures reached a minimum of −6° F. the bark temperatures were about 10 to 12° warmer; and when air temperatures began to rise from this point, the bark warmed more slowly and for a short time was even colder than the air."

The next comparison of air and bark temperatures during subzero cold periods was made by Beal (*3*, *U10*) in February 1933. Using bulb thermometers and the same technique as Rust, he obtained a series of hourly readings from six infested trees on Ochoco National Forest over a period of 66 hours. At a minimum air temperature of −26° F., minimum bark temperatures ranged from 8° to 20° higher. This range was largely attributed to differences in bark thickness. The spread between bark and air temperatures was much greater in thick-barked trees. In bark one-half inch thick, the minimum temperature reached was 8° higher than the air temperature; but in bark from 1⅝ to 2 inches thick, the bark was 26° to 29° warmer.

Beal (*3*) also found that the lag of bark temperatures behind changing air temperatures increased with bark thickness. In bark one-half inch thick, temperature lagged 1 hour behind rising or falling air temperatures; but in bark 2 inches thick, the lag was 2 hours. In summarizing Beal stated: "The spread between air and bark temperatures is governed chiefly by bark thickness and the rate of temperature change. The lag in reaction of bark to air changes depends principally upon bark thickness."

A study of comparative bark and air temperatures was started on Modoc National Forest in 1935, using specially designed Foxboro anti-ambi compensated thermographs that gave a continuous record of bark temperatures. The bulbs were installed in the bark at 10 feet above the ground; a Friez hygrothermograph recorded air temperatures at a nearby point (fig. 19). Three bark temperature records and one air temperature record were maintained through three consecutive winters; in addition, minimum bark temperature records were obtained from seven infested trees within the same area.

Salman and McLees (*U289*) reported:

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FIGURE 19.—Recording thermometer and emergence cages placed on ponderosa pine to determine effect of temperature on emergence of the western pine beetle.

1. A close association exists between minimum air temperatures and minimum bark temperatures. [A correlation coefficient of 0.953 was found.]

2. Minimum bark temperatures may be estimated from minimum air temperatures (at least through the range of temperatures included in these tests, which ranged from +61° F. to −30° F.) with an accuracy equal to a standard error of estimate of ±4.70° F.

3. By elimination of one or more of the chief factors that contribute to the error of estimate, it is possible to reduce the standard error by from 0.6 to 2.9° F. Of these factors, daily temperature trends, variations in the conditions surrounding and inherent in individual trees, and the amount of daily temperature range appear to be the most important. Each of the last two factors contribute approximately one-fourth of the standard error of estimate.

4. The relation of minimum air to minimum bark temperatures changes along the temperature scale. [At Hackamore, Calif., with minimum air temperature of 60° F., the bark was 11° warmer; at −30° the minimum bark temperature was 24° higher.]

5. The relation between air and bark temperatures is statistically very highly significant. A similar clear relation seems to exist between mortality and bark temperature or the temperature of exposure.

Tests of brood mortality at given temperatures of exposure showed a standard error of estimate of ±4.87° F. or a range of about 9 percent. Salman and McLees (*U289*) concluded: "It is not established . . . that brood mortality can be estimated from air temperature records without considerable error. Such estimates will be of most value when temperatures are low enough to produce considerable mortality and of least value when they produce but slight mortality."

Relation of Bark Thickness to Brood Mortality

In many of the field studies of brood mortalities after cold weather, the temperatures reached in the bark were unknown, but a great deal of work has been done to relate mortality to bark thickness. In appraising the effects of the low temperatures of December 1932 on the Modoc National Forest, Salman (*U262*) analyzed 115 bark samples containing 6,543 dead and living larvae and found a fairly consistent relation between bark thickness and brood mortality. In samples where the bark was one inch or less thick, the mortality of larval broods averaged 99.5 percent. In bark 2 to 2¼ inches thick, the mortality averaged 39.4 percent. Bark samples of intermediate thicknesses showed mortality ranging between these extremes.

Keen and Beal (*U170*) studied bark thickness as a factor in mortality of broods after the 1932–33 subzero temperatures in Oregon. They examined 1,200 bark samples totaling 782 square feet and containing 147,619 living and dead larvae. Bark thicknesses proved to be the most important factor modifying the effects of air temperatures. Mortality varied inversely with bark thickness; for the same temperatures within the critical range, the thicker the

bark the lower the mortality. The texture of the bark, whether hard and flinty or soft and spongy, also appeared to be important; a much higher survival of brood was found in spongy bark.

Yet on the whole, bark thickness is not as important as might be expected. Keen and Beal (*U170*) found that in eastern Oregon practically 95 percent of all pine bark is from 5/8 to 1½ inches in thickness. The occasional extremes below and above this range therefore can have only small effect in modifying the overall average mortality. However thick bark is of extreme significance in survival of the species.

In a report upon the effects of the 1932–33 freeze in northern California, Furniss (*U66*) stated:

> It has been observed in trees with very thick bark, often deeply ridged, that the brood tends to become localized in the vicinity of the crevices, thus tending to lessen the effective protective layer. Thus it is conceivable that a tree of uniform (bark) thickness might protect the brood to a greater extent than a tree with deeply ridged bark but of much greater average thickness.

Furniss (*U69*) also found that mortality generally varied inversely with bark thickness, in the November 1935 cold spell when the temperature dropped to −27° F. in eastern Oregon. An exception was that broods with only one-fourth inch of bark insulation suffered less than those with half-inch insulation. Mortality was related to the position of brood with reference to the inner bark surface—the nearer the inner bark surface, the greater the mortality. About 90 percent of the overwintering third and fourth instar larvae occurred within one-fourth inch of the inner bark surface.

Keen and Furniss (*81*), taking into account the depth of larval broods, determined that "in central Oregon more than 90 percent of the overwintering brood are protected by 1 inch or less of bark." In summarizing all of the mortality studies of preceding years, they concluded:

> In general, mortality from freezing varies inversely as thickness of the insulating bark over the brood, although the correlation is not good for insulation of less than one-half inch.

But they also found that a higher mortality occurred among larvae living in or near the phloem area than in the outer bark, regardless of the fact that the larvae in the phloem were protected by a greater bark thickness. This difference was attributed to two factors: the high moisture content of the phloem, which has been shown to affect the cold resistance of broods unfavorably, and the small larvae in the phloem region, which do not develop the same degree of cold hardiness as mature larvae.

Duration of Cold Periods

As in the laboratory experiments, fieldworkers found that time was highly important in modifying low-temperature effects. The longer subzero weather prevails, the more nearly do bark temperature and body temperature of larvae tend to come into equilibrium with air temperature. Keen and Furniss (*81*), in reporting upon three periods of cold weather, stated: "The data, although not conclusive, indicate that, given the same minimum temperatures the

prolonged cold was most effective, the unseasonable cold less effective, and the brief cold least effective in reducing western pine beetle populations."

Moisture Conditions in the Bark

Miller (*95. U197*) found that larval broods in saturated bark succumb to temperatures some 10° higher than broods in normal dry bark. That excess moisture may reduce the degree of cold hardiness seems reasonable in view of the theory that the insect must regulate the amount of free water in its body tissues and reduce water content of the cells in order to avoid freezing. As suggested by Keen and Furniss (*81*) this factor may overbalance that of bark insulation and explain the high mortality of young larval broods in the phloem area. On the Ochoco-McKay Creek control project in central Oregon during the winter of 1932–33, it was in dry partially abandoned trees that broods survived best. According to Keen (*U150*):

> The heaviest loss from winter killing occurred in the broods of small larvae in the inner, moist bark of green trees. Thus small larvae in the moist inner bark, close to the wood and supposedly protected by a thicker layer of bark were killed more readily than full grown larvae in the outer, dry bark, with apparently much less bark protection.

Topography, Elevation, and Wind Movements

The distribution of minimum temperatures within a general watershed of 138 square miles on Ochoco National Forest, Oreg., was studied by Keen (*U156, 79*) to determine whether standard Weather Bureau records usually taken at towns and population centers could be used as a reliable index to bark beetle mortality in nearby forested areas.

Two cold periods were studied: one during November 1936 and another in January 1937. On November 2, 1936, the temperature dropped to 5° F. and on January 8, 1937, to −27° at Ochoco Ranger Station. A limited examination by Buckhorn and Furniss (*U41*) showed 46 percent of the large western pine beetle larvae were killed. The low temperatures occurred during clear, still nights with little or no wind movement. This brought about a typical temperature inversion, with the coldest layers of air settling in the valleys and warmer air moving to the higher levels. This was in direct contrast to a cold period of December 1932 when a cold air mass moved in and "a strong wind blew more or less constantly, resulting in a thorough agitation of the air, so that similar temperatures prevailed over wide areas."

Because of the temperature inversion in 1936 and 1937,

> Valleys were consistently colder than slopes or ridges, but the differences between south slopes and north slopes were so slight that they could hardly be considered significant. Ridges tended to be colder than slopes.

The total spread in temperature between the 144 thermometers used in the experiment was 19° F. in the November cold spell and 22° in the January cold period. The maximum difference between any one

reading and the temperature at Ochoco Ranger Station (within the area) was 13°. The greatest average difference of any one elevational zone and Ochoco base weather station was 10.8°. On the average, the forested area was about 5° warmer than the valley where the base weather station was located, but only 1.7° to 2.5° warmer than the nearest standard weather station at Prineville, Oreg., some 27 miles distant.

In summarizing this study, Keen (*U156*) stated that:

> This low temperature experiment showed that during cold spells without wind movement there may be wide temperature differences throughout a drainage area of 138 square miles, sufficient to cause considerable variation in bark beetle mortality within the area, but that for the forest area as a whole the average temperature may be reasonably close to that shown by nearby standard weather stations. If the average low temperature differential between a given forest area and its nearest standard weather station is determined, then it should be possible to estimate the general bark beetle mortality on the area following a cold period with a reasonable degree of accuracy.

Also (*79*):

> It is reasonable to expect that smaller differences might have occurred if the cold periods had been due to invasion of polar air masses rather than to heat loss through radiation and temperature-inversion conditions.

Height on the Tree

During periods with quiet air and an inversion, the temperature is colder near the ground than higher in the trees. In the central Oregon study Keen (*U156*) found, "a significant difference between the 10-foot level and the higher levels, but no significant difference between the 40- and 70-feet levels. These higher levels tended to be from 0.5 to 0.7° F. warmer than the 10-foot level."

During freezes caused by cold air masses accompanied by high winds, temperature inversion does not occur. Then, Keen and Furniss (*81*) found, "winter killing at the base of trees averages 19.7 percent less than the general average for the entire tree. Above the base, the mortality rate is uniform for bark of the same thickness." The difference in mortality may be due to warmer temperatures near the ground or possibly to the character of the bark, since bark of the same thickness was compared.

North and South Exposures on Trees

Keen (*U156*) found no difference in temperature between the north and south sides of trees during two periods of extremely low temperature when the air was still. Keen and Furniss (*81*) found a significant difference in brood mortality after freezes with strong wind movement:

> Brood mortality is consistently greater on the north than on the south side of infested trees, following periods of very cold weather. This is well illustrated by a statistical analysis . . . of 145 trees sampled in the winter of 1932–33 . . . mortality on the

north side was found to be 30 percent greater than on the south side.

Minimum temperatures reach about the same level on both sides, but on bright days temperatures do not rise as rapidly or as much on the north as on the south side: therefore the duration of cold is much longer on the north. The second consideration is that because of generally colder conditions on the north side, brood does not develop as rapidly as on the south side. Overwintering larvae are smaller and in addition the bark is tighter and more moist.

Beal (*U10*) found that during bright days of subzero weather, heat from the sun warmed the bark on the south side as much as 16° above the air temperature.

Tightness and Texture of Bark

Furniss (*U69*) observed that "Broods in trees with tight bark are less resistant to freezing than broods in trees with loose bark." This difference is probably due to a correlation between tight bark, its moisture content, and younger age of brood. Bark texture was considered to be unimportant.

General Effect of Low Winter Temperatures on Bark Beetle Populations

Despite the many modifying factors, the overall effect of low winter temperatures in killing western pine beetles can be estimated with reasonable accuracy. From a large number of examples of minimum air temperatures and the corresponding brood mortality found during three periods of cold weather in eastern Oregon—a period of prolonged cold in December 1932, a short period of intense cold in February 1933, and a period of unseasonable cold in November 1935—Keen and Furniss (*81*) showed that a fairly close relationship existed between minimum air temperatures and percent mortality (fig. 20). It is evident from figure 20 that within rather broad limits the amount of brood mortality can be estimated if the minimum temperature is known. This chart should be helpful in estimating the probable effect on western pine beetle populations of any low winter temperatures reported by the Weather Bureau from ponderosa pine forest areas.

Although severe cold spells have caused very high mortality, western pine beetle populations were not eliminated. They were greatly reduced at first but have shown an amazing capacity to recover their numbers within a year or two.

In appraising the effects of the 1932–33 winter kill in both Oregon and California, Keen and Furniss (*81*) stated: "For the entire area affected, the 1933 infestation was lower than in 1932, and considerably lower than it would otherwise have been, as indicated by the general infestation trend." They added, however:

> . . . the effects of low temperatures are not evident in the infestation trend except in extreme instances, about once in 10 years, when the course of the infestation may be altered for about 1 year. . . . Anything less than 50 percent reduction has little

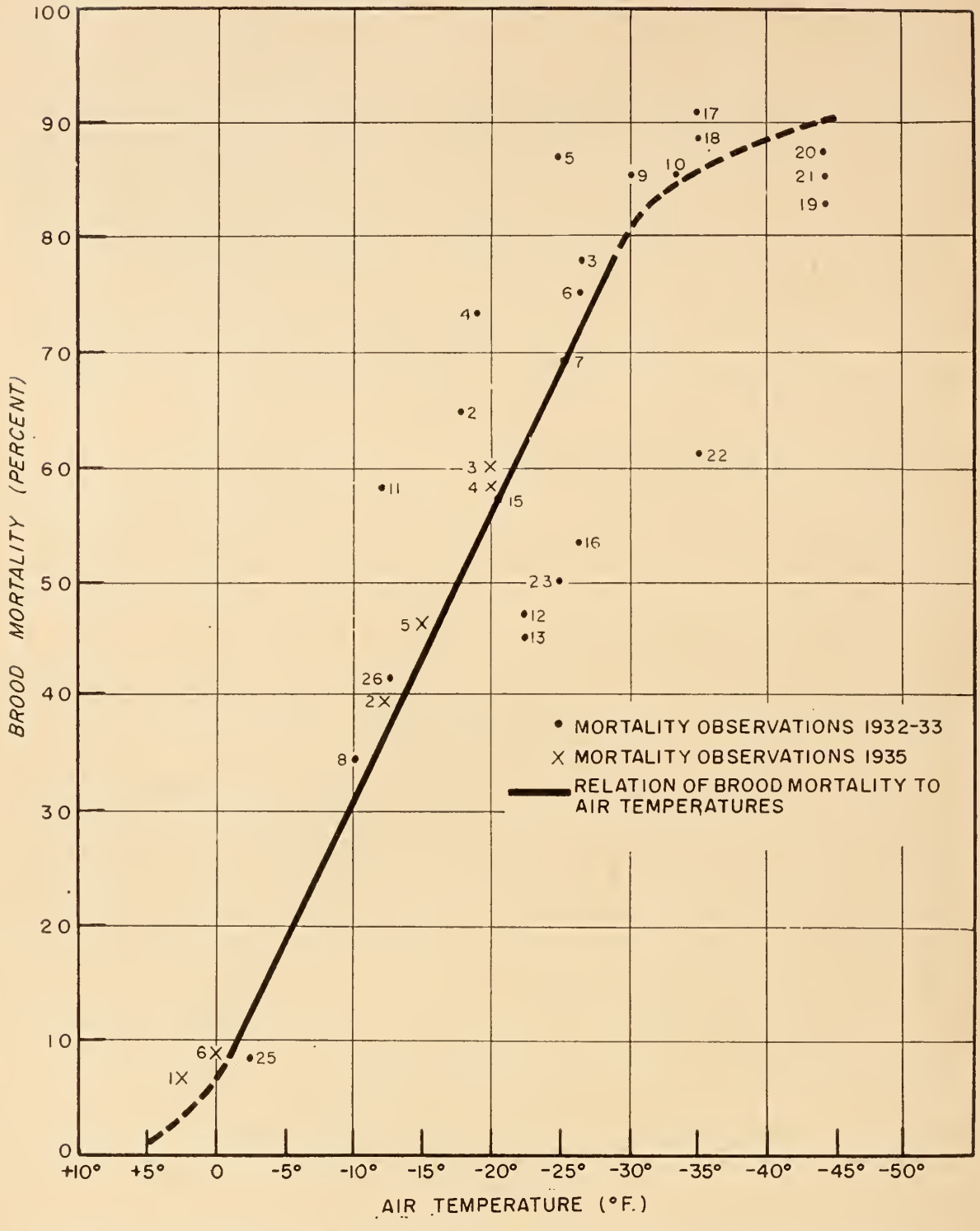

FIGURE 20.—Relation of air temperature to western pine beetle mortality.

or no effect upon the annual infestation; therefore, this amount of kill, or more, is necessary to cause alteration of artificial control work.

Lethal High Temperatures

In 1915 Keen (*U130*) noted that no beetles emerged from the top of an infested log lying exposed to the sun. Yet there were exit holes on the underside. He concluded that "the bark becomes so heated in the summer sun that the beetles either fail to develop or are killed." He also tested the effects of solar heat upon the adults:

"One hundred fifty *D. brevicomis* were placed on a pine board in the sun. All died within about 20 seconds. The air temperature was about 95° F., but the board was considerably hotter."

Following this first observation, the possibility that solar heat could be used in the control of the western pine beetle was apparently overlooked until 1919. During the late spring of that year the exposure of infested bark to the sun was incidentally used to destroy broods on a control project in Sequoia National Park. As the hazards of burning infested bark increased in late April and May, a number of infested trees that had been felled and peeled were held awaiting more favorable weather for burning. It was noticed that broods in pieces of bark exposed to the sun died within a few days. All of the infested bark was then spread out in the sun, and practically all of the broods were killed without burning.

The prospect that solar heat could be used in lieu of burning stimulated a series of experiments near Ashland, Oreg., by Miller (*U185*) and Patterson (*U215*). In 1920 and 1921 further experiments with high temperatures were carried out near North Fork, Calif.; the results were later included in a summarization of the work on high and low lethal temperatures published by Miller (*95*).

Critical High Temperatures.—Laboratory studies showed that exposed larvae first revealed the effects of heat at temperatures of 95° to 100° F. when sluggishness and decreasing activity set in. Above 100° activity ceased, but death did not immediately occur. When larvae were exposed to currents of warm air, which produced low humidity and rapid evaporation, they became paralyzed; after 30 minutes exposure to temperatures of 100° to 105°, they did not recover.

When normal humidity was maintained in sealed containers, simulating conditions in the larval and pupal cavities in the bark, high temperatures took effect more slowly. Slight larval activity continued up to 105° F. Paralysis set in after several hours exposure at 108° to 110°, but the larvae were able to recover when brought back to normal temperatures. Above 110° the temperatures usually were fatal. Paralysis set in after 20 minutes exposure at temperatures between 110° and 115°, and there was no recovery when normal temperatures were resumed. No larvae survived even brief exposures at 118°.

Field tests were made by exposing infested bark sections to the sun and recording bark temperatures by means of mercury bulb thermometers imbedded in the bark. Noticeable mortality first appeared when the bark temperature reached 100° F., and all larvae were killed when the temperature reached 120°. This indicated a fairly wide range of critical high temperatures. The following records are from a typical test between the hours of 9:30 a.m. and 11:30 a.m. on June 23, 1920:

Time (a.m.)	Bark temperature (°F.)	Mortality (percent)
9:30	76	1.3
10:00	100	34.2
10:30	109	78.0
11:00	118	94.0
11:30	120	100.0

During this test, air temperatures ranged from 78° to 80° F. Because of variations of bark thickness and moisture, the temperatures throughout the bark probably differed from those recorded by the thermometers; this may account for the differences between mortalities in the field and at similar temperatures in the laboratory. It is fairly well established, however, that the critical high temperatures for larvae range from 100 to 115°.

Beal (*U6*) found that sustained high temperatures between 102° and 106° F., were fatal to all eggs.

Effect of Solar Heat on Broods in Infested Trees.—There is little or no evidence that appreciable mortality occurs in beetle populations in their natural environment in the bark of standing trees as a result of hot weather. The bark surface of such trees is vertical in position so that through the hottest part of the day there is a high angle of incidence to rays of the sun. Experiments showed that to absorb a great amount of solar heat, the bark must be exposed with its surface approaching a right angle to the rays of the sun. Also, infested bark of standing trees is usually shaded through part of the day by limbs and foliage, and when it is exposed to the sun, the insulating thickness of the bark protects the brood long enough to prevent fatal temperatures.

Some mortality may occur, however, when infested trees fall so that the prostrate trunk is exposed to the midday sun. This happens rarely in nature. When green trap logs are attacked after they fall, the beetles attack only the underside of the log or shaded bark areas, and no brood develops in that part of the log exposed directly to the sun.

Nutritional Deficiencies

The part that unsatisfactory food conditions may play in bringing about mortality of broods has not been investigated. It has frequently been observed that certain trees produce bigger and more vigorous beetles in greater numbers than others, probably, one can reason, because of varying nutritional conditions. But since information on nutritional requirements of the western pine bettle is very limited, the reason can be nothing more than conjecture.

Competitiou for Food Supply

The most important feeding period for insects is during the larval period. When food is limited, some must inevitably die of stravation. This is especially true of the western pine beetle, whose larvae exist within a very small area. The female largely determines this area when she deposits her eggs. The young larva must find its entire food supply within an inch or two of the egg niche where it begins its existence. It is not able to shift to a new location if the food supply in the inner bark is inadequate.

Competition Between Individuals of the Same Broods

Usually attacks by parent adults are spaced over the bark surface of a tree so that food is adequate to carry the broods through complete development. At times, however, an apparent overcrowding of attacks has been noted. This has occurred when there was a high concentration of adults, as during a period of epidemic in-

festation. Then, attacks and egg galleries were very closely spaced, and larval mortality was high. One such case was reported by Miller (*93*) in the California windfall area in 1921. Here the attack was estimated to be about twice as heavy as normal and the emergence of new adults about half of normal. It was inferred that the broods were reduced as a result of starvation.

Furniss (*U68*) found some evidence in Modoc County, Calif., that after the severe freeze of 1932, western pine beetle attacks spread out in 1933 and produced more progeny per attack than usual. He stated: "More than four times as many beetles emerged from the light attacks than did from heavy attacks . . . When an infestation is at a low ebb in a stand containing numbers of susceptible trees, as in the case on the Modoc in 1933, there is an abundance of food per beetle. This results in the spreading out of attacks until each pair of beetles has approximately the area best suited for development of their progeny."

Keen (*U142*) plotted the number of beetles attacking and emerging during a 10-year period on the Jenny Creek unit of southern Oregon from 1917 to 1926 and concluded that ". . . to some extent at least, the emergence is influenced by the number of beetles attacking . . . a low attack producing a low emergence and vice versa. These records do not indicate that overcrowding of attacks, such as occurred in 1925 is detrimental to good brood development." The effect of overcrowding of attacks upon brood development has not received the critical study necessary to arrive at a firm conclusion as to its influence as a natural control factor.

The great variation that has been found in the number of beetles emerging from a square foot of bark, regardless of the number that attack, leaves some doubt as to what constitutes "normalcy." The actual number of larvae per square foot that can be adequately nourished is not known. On the whole, it can be assumed that overpopulation occurs rarely. The parent beetles usually have ample opportunity to disperse their attacks, both in the trees and over the forest, so that their progeny are assured of ample food supply.

Competition With Other Cambium-Feeding Insects

The larvae of large beetles that attack infested trees and feed in the phloem area become a competing factor when they consume the food supply of the inner bark before it can be utilized by bark beetle broods. Most of the competition from this source has been attributed to the cerambycids. Hopkins (*44*) first recognized the importance of these beetles: "The so-called robbers consist of large bark-boring grubs or larvae of long-horned beetles (Family Cerambycidae) which sometimes rob the bark beetle larvae of their food supply or kill them outright, by destroying the inner bark before the broods of bark beetles have completed their development." Blackman (*5*) found the ponderosa pine bark borer (*Acanthocinus spectabilis* Lec.) especially effective as a robber of the Black Hills beetle. He also listed the spotted pine sawyer (*Monochamus maculosus* Hald.), the black spruce borer (*Asemum atrum* Esch.), and the western larch roundheaded borer (*Tetropium velutinum* Lec.), but considered the latter two species of lesser importance since "they are

considerably smaller, do not occur in so many trees, and are found principally in the lower trunk."

In referring to the ponderosa pine bark borer, Keen (*62*) stated that the "larvae feed in the inner layers of bark, often consuming so much of it as to starve out the bark-beetle broods."

Person (*U241*) compared emergence of the western pine beetle from bark that had been heavily mined by cerambycids with emergence from bark in which there was little or no cerambycid work. From 4 trees he selected 34 square feet of bark and reported:

Sq. ft. of bark	*Inner bark mined by borers (percent)*	*Beetle attacks per sq. ft. (number)*	*Beetle emergence per sq. ft. (number)*
17	8	14	60
17	56	12	37

He concluded that "the averages for the 4 trees show that the emergence from sections with little or no cerambycid work was almost twice as high as from sections on which the cerambycids had destroyed on the average about 56 percent of the inner bark." Person attributed all of the borer work to the ponderosa pine bark borer.

> As these larvae were a number of times larger than *D*[*endroctonus*] *b*[*revicomis*] larvae, they would naturally destroy large quantities of their food and would probably kill many of the *D.b.* outright when they happened to get in the way of their (the cerambycids') large mandibles. . . . To be of importance they must begin work in the phloem while the *D.b.* brood is still small and before it has worked out into the outer bark where it is safe from the cerambycids.

In 1933 Furniss (*U67*), working with J. W. Bongberg, made a preliminary study of the life history of the ponderosa pine bark borer. He found that this species and *Acanthocinus obliquus*, a smaller gray species, both infest about the same bark area that is attacked by the western pine bettle. "*A. spectabilis* characteristically infests the lower bole where the bark is thick while *A. obliquus* is commonly found in the upper portions of the stem where the bark is thin." Available data in one case indicated that the ponderosa pine bark borer had developed and emerged in 4 months. Most of the brood, however, apparently requires 1 year to complete the life cycle. Furniss concluded that:

> The effectiveness of *Acanthocinus* as a control factor of the pine beetle is bound up directly with its ability or inability to follow *Dendroctonus brevicomis* into the trees almost at once and to develop rapidly. The fact that the pine beetle larvae mine into the outer bark (soon after) hatching makes the Cerambycid work much less a natural reduction factor than when in association with a species such as the Black Hills beetle, the broods of which confine their activities to the phloem region almost entirely.

Insect Parasites

The records accumulated over a period of some 30 years fail to indicate that parasitism plays an important part in the natural control of the western pine beetle. In fact, records of specific parasitism are rare, although investigators have persisted in the search for evidence.

Webb (*144*) does not mention parasites but does refer to the work of the clerid predator. Hopkins (*44*) mentions parasites only in a general way in discussing the natural control of bark beetles (*Dendroctonus* spp.). The first records of what were thought to be specific parasites were made by Keen (*U130*) when he suspected three species of chalcids as being parasites of the beetle because they belong to a group of insects which are mainly parasitic and were found either ovipositing in, or were reared from, bark infested by the western pine beetle.

Later collections and rearings of these same species of parasites by other investigators confirmed the fact that they are found occasionally with western pine beetle broods and that they are probably true parasites. Person (*U240*), summarizing available notes on parasites of western pine beetle up to 1928, concluded that "a few parasitic species are almost always found with *D. brevicomis* but not in sufficient numbers to be of much importance." Miller (*U200*) in 1943 summarized all available records on probable parasites and obtained the following information:

1. *Cecidostiba burkei* Cwfd. has been found ovipositing through bark infested by *D. brevicomis* broods and has been found in cages containing infested bark in rearing. One case is recorded of the adults being taken from pupal cells of *D. monticolae* in lodgepole pine with remains of host. It has also emerged in cages containing sugar pine logs infested by *D. monticolae.*

2. *Cecidostiba dendroctoni* Ashm. has emerged in a cage containing bark infested by *D. brevicomis*; was also found on brood log of *Scolytus ventralis.*

3. *Eurytoma* sp. was found ovipositing in bark infested by *D. brevicomis* and was reared from bark infested by flatheads. It may or may not be parasitic as the species of this genus vary from parasitic to phytophagous.

4. *Pachyceras eccoptogastri* Ratz. The best case for parasitism has been established for this species. It has been found ovipositing in, and has also been reared from, bark infested by *D. brevicomis.* In two cases larvae and pupae were isolated from larval cells of *D.b.* and reared through to adults. One record indicates that it is also parasitic on *Ips oregoni.*

The total number of notes collected since 1915, representing intensive work by a number of investigators, records only 19 cases of suspected parasitism. This scarcity of records over many years can be interpreted as evidence that parasites are a negligible factor in the biological control of the western pine beetle.

Predators

Predators, on the other hand, are common. Birds and a long list of predatory insects are undoubtedly an important factor of natural control.

Birds

The work of woodpeckers on advanced larvae and pupae in the outer bark of infested trees attracted the attenion of the first investigators. Webb (*144*) observed that "the work of woodpeckers was found upon most of the trees which had been killed by *D. brevicomis*, and these birds had evidently destroyed a large per-

centage of the insects in some of the trees." Hopkins (*44*) discussed the importance of bird predators, but concluded that "birds evidently render the greatest service where but few trees are being killed . . . where many hundreds of thousands of trees are being killed, the limited number of birds can have little or no effect."

During the western pine beetle control projects on Klamath National Forest in California, 1911–12, records were kept on the abundance of woodpecker work in all treated trees. Burke (*U42*) summarized the records from 679 trees and found that the amount of woodpecker work had been light on 13 percent, medium on 39 percent, heavy on 1 percent, and none on 47 percent of the trees.

Keen (*U130*) undertook to determine the percentage of brood destroyed by woodpeckers. He compared the emergence from bark samples that had been heavily worked by woodpeckers with the emergence from unworked bark and found that the woodpeckers had reduced the brood by about 73 percent.

Buckhorn (*U38*) investigated the effectiveness of woodpeckers on western pine beetle broods on Ochoco National Forest of Oregon in 1934. He placed a 2-foot cage over bark that had been 70 to 85 percent pecked and reduced from 1¼ to ¼ inch or less in thickness. Next to this was a similar cage covering undisturbed bark. From bark unworked by woodpeckers, 370 beetles per square foot emerged. From bark worked by the woodpeckers, 103.5 beetles per square foot emerged—a reduction due to woodpecker feeding of 72.1 percent (fig. 21).

Patterson (*U220*) pointed out that the woodpeckers feed not only on bark beetle broods, but also on larvae of cerambycids and buprestids in the bark. Woodpeckers destroy the greatest percentage of bark beetle broods during the winter months when the insect is in the larval stage and dormant.

Patterson was of the opinion that the most important woodpecker predators of the western pine beetle were the following (in the order named):

1. White-headed woodpecker (*Dendrocopos albolarvatus*)
2. Modoc woodpecker (*D. villosus orius*)
3. Gairdners woodpecker (*D. pubescens gairdnerii*)
4. Arctic three-toed woodpecker (*Picoides arcticus*)
5. Williamson's sapsucker (*Sphyrapicus thyroideus*)
6. Western pileated woodpecker (*Dryocopos pileatus picinus*)

All of these species are more or less common in the transition zone of Oregon and California.

Woodpeckers also feed on beneficial insects as well as the destructive ones. Person (*U238*) studied woodpecker activities on the Sierra National Forest, Calif., in 1926, giving special attention to the extent to which these birds feed upon the beneficial clerid and ostomid insects. The species of woodpeckers feeding on infested trees in this area during the spring, summer, and fall period were the western pileated woodpecker, the white-head woodpecker, and the hairy woodpecker (*Dendrocopos villosus*). Person concluded that the western pileated woodpecker was the most beneficial when it was abundant because it thoroughly chiseled off the outer half to three-quarters of the bark over large areas. He compared brood counts from bark sections that had been worked by this woodpecker with unworked sections and found that in the former the surviving

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FIGURE 21.—Outer bark of ponderosa pine riddled by woodpeckers in search of larval broods of the western pine beetle.

brood was only 16 percent of normal. He also found that the bird had reduced the clerid predator population until it was 30 percent of normal.

The hairy and white-headed woodpeckers were found to be less thorough in working over the bark and were inclined to take only those insects nearest to the bark surface. A stomach examination of each species showed that they feed indiscriminately upon the western pine beetle, clerids, cerambycids, and other associated injurious and beneficial insects.

In three trees, Person (*U238*) found that the hairy and white-headed woodpeckers fed upon the black-bellied clerid (*Enoclerus lecontei* Wolc.), which pupates near the bark surface, more often than on broods of the western pine beetle, which were deeper in the bark. In counts from 136.5 square feet of bark from these three trees, he found that the woodpeckers destroyed nearly 10 percent of the beneficial clerids and only a negligible percentage of broods of western pine beetle.

Many groups of insectivorous birds may feed on beetles during the flight period, but only the woodpeckers are known to feed on broods in the bark.

Mammals

Rust (*U253*) found that when broods of mountain pine beetle were exposed by peeling bark from the trees the broods were either carried off by ants and centipedes or were eaten by small mammals, such as chipmunks and mice. There is little possibility of rodents feeding on the western pine beetle, because broods are effectively protected by the outer bark. Rodents may capture a few adults of the western pine beetle while they are on the ground or in the duff during the attack period, but evidence of this habit is yet to be obtained.

Insect Predators

Insects that prey upon the western pine beetle have been the subject of much detailed investigation. Clerid beetles aroused the interest of early investigators, probably because of the conspicuous habits of the adults in concentrating on trees that are being attacked by bark beetles. On newly attacked trees, clerid beetles run actively over the bark surface and capture bark beetle adults (*Dendroctonus* spp.) before they burrow into the safety of the inner bark. In 1892–93, Hopkins (*41*) was so impressed with the European bark beetle destroyer, *Clerus formicarius*, that he introduced it into West Virginia to work on the southern pine beetle (*Dendroctonus frontalis*). The imported predator, however, apparently did not thrive in its new environment.

In the first studies in Idaho, Webb (*144*) reported that "larvae of the predaceous beetles of the genus *Clerus* (*Enoclerus*), which are known to prey upon *Dendroctonus* larvae, were quite common in and under the bark of the infested trees, and they doubtless help to some extent in keeping down the numbers of the bark beetles."

Detailed studies of the predaceous insect enemies of the western pine beetle were begun in 1922 in connection with the Southern Oregon-Northern California Pine Beetle Control Project at Klamath Falls, Oreg. In a preliminary report on these studies Person (*U233*) listed some 10 species of beetles and one Rhaphidid which observations indicated to be predaceous on bark beetles (*Dendroctonus* spp.). This report included life history notes and the results of feeding experiments with the more important predators. Person pointed out that under the methods then used in direct control work, i.e., peeling and burning all infested bark, beneficial insects were destroyed as well as the bark beetles. This discovery led to the practice of protecting from fire the bark and duff around the stump where the clerids concentrate to pupate.

Person's studies were continued at North Fork, Calif., in 1923 and 1924 (*U236*) to determine the capacity of the different insect predators to consume adults and larvae of the bark beetle. Miller and Person (*U206*) reported a positive correlation between the mortality of western pine beetle brood and the number of predators per square foot of bark at different heights on a tree.

Person (*U240*) summarized all of the work that had been done up to 1928 on parasites and predators of the western pine beetle and gave a complete account of the habits and seasonal history of the black-bellied clerid. He also described experiments to determine the

actual effectiveness of this species as a predator. In 1928, 1929, and 1930 the work was concentrated on this species and a series of experiments was conducted in biological control.

The Blue-Green Trogositid (Temnochila virescens var. chlorida (Mann.))

The blue-green trogositid is the most commonly observed predaceous insect in or around trees infested by bark beetles. The adult of this ostomid beetle is from 10 mm. to 18 mm. long and of an iridescent bluish-green color. The adults appear on infested trees soon after a tree has been attacked. They usually are found in bark crevices or on the surface and actively prey upon any unwary bark beetles that may be loitering on the bark surface.

This species is by no means specific in its predation on the western pine beetle. It will be found on trees infested by many species of bark beetles, cerambycids, buprestids, and other wood-boring and cambium-feeding insects. The larvae, which are also voracious general predaceous feeders, are grayish-white at maturity and 25 to 30 mm. long. The head is black and flattened, the dorsal surface of the first three thoracic segments have black sclerotized plates, continuous on the first two segments and separated on the third. The dorsal part of the last abdominal segment has a black hooklike process.

The habits and seasonal history have been worked out by Person (*U240*) and Struble (*126*). The eggs are laid in groups of from 2 to 50, usually deep in bark crevices. According to Person (*U240*), who studied this species only in connection with the western pine beetle:

> After hatching, the larvae work their way through to the inner bark, taking advantage of cracks between the bark scales and the entrance and ventilating holes of *D. brevicomis*. After reaching the inner bark, they begin to feed on the young *D.b.* larvae, following them as they work back into the middle of the bark. The larvae develop with the *D.b.* and feed upon the larvae, pupae, and new adults. They burrow their way through the bark at will, going from one *D.b.* to the next while feeding. They are cannibalistic in the larval stage. Only the larvae which hatch by July 1 complete their development during one season at Klamath Falls. The larval period varies from about 3 or 4 months for those that complete their development in one season to 10 or 11 months for those that overwinter as larvae.
>
> The pupal stage is passed in an unlined cell in the middle of the outer bark at the place where the larvae finish feeding. The pupal stage of the individual lasts about 2 weeks (10 to 20 days).
>
> The adults overwinter in the bark crevices of infested trees. The average adult life is about 4 months for those that do not overwinter, and about 10 to 12 for those that do.

Both Person (*U240*) and Struble (*126*) found the adults of the blue-green trogositid to be voracious feeders. In confinement they consumed from 1 to 3 mountain pine beetle adults per predator in a 24-hour period. Frequently as many as 15 adult bark beetles were killed, and many of these were eaten in a day by 1 large tro-

gositid adult. Person found that in cages the average life of adults was more than 3 months when fed on adult western pine beetles; the average number of beetles consumed over a long period was 0.935 daily. Person also observed that trogositid adults fed on clerids and probably any other insect they could capture. Although this species was at first thought to be the most effective predator of the western pine beetle, it was finally found to be ineffective because of its indiscriminate selection of hosts and its cannibalistic tendencies.

The Black-Bellied Clerid (*Enoclerus lecontei* Wolc.)

The black-bellied clerid is predaceous on various species of engraver beetles (*Ips* spp.), twig beetles (*Pityophthorus* spp.), and bark beetles (*Dendroctonus* spp.), but in California, Oregon, and Washington it is found most abundantly with western pine beetle broods. Its biology and its effectiveness as a predator of the western pine beetle have been adequately covered in an article by Person (*113*).

The adults are very active and voracious and run rapidly over the bark surface during the period while trees are being attacked by the western pine beetle. Their movements somewhat resemble those of ants, although the clerids are more active. They grasp the pine beetle and suck the body juices, discarding the hard chitinized parts of the body. According to Person (*U240*), each clerid adult destroys at least 25 pine beetles during its active life of 6 to 8 weeks.

The eggs are laid on newly attacked trees in the tiny crevices between the bark scales. Usually from 2 to 5 eggs are laid in a group, but as many as 10 have been found closely fitted together in a one-layered mass. Incubation requires from 10 to 14 days under average conditions of the active field season.

The larvae of the black-bellied clerid are pink in color, with characteristic anal hooks and scleritized parts dark brown. Upon hatching they enter the outer bark through a crevice or ventilation hole and are next found in the phloem or inner bark. Here they begin feeding on newly hatched western pine beetle larvae, working their way through the bark from one larval mine to another, killing their victims and consuming all the strongly scleritized body parts. As the western pine beetle broods develop and enter the outer bark, the clerid larvae follow them, and by the time the host larvae are mature, the clerid larvae have completed their feeding. Then, from 40 to 90 percent of the clerid larvae bore out through the bark and crawl to the base of the tree where they pupate in the outer bark scales near the surface of the ground or in duff surrounding the stump. The remaining 10 to 40 percent remain where they completed their feeding, and pupate in the outer bark of the main trunk.

The pupae are formed in flattened oval cells hollowed out by the prepupal larva. These cells are lined with a white silvery substance which distinguishes them from the bare unlined cells made by the blue-green trogositid. The pupal period lasts from 6 to 14 days under active temperatures.

The seasonal history (*U240*) of the black-bellied clerid is rather complicated and is only partially synchronized with that of the

western pine beetle. In central California there are about two generations, but a certain percentage of the broods is retarded in development, with the net result being equivalent to a single generation. Their overwintering habits are such that clerids concentrate on the first generation trees of the western pine beetle. Person reports that the average number of clerid larvae per square foot of infested bark on first generation trees is nearly double the number found in trees of the second generation, and more than three times the number on trees of the third generation.

Person obtained some data on the effectiveness of this clerid as a predator by artificially infesting trees with western pine beetle adults and excluding the clerids by means of cages. The final emergence of adult pine beetles in the cages was compared with that of normally infested trees to which the clerids had free access. In cages where the clerid population was reduced to 1.5 larvae per square foot, emergence of bark beetles was 146 per square foot; outside the cages, however, the population of clerid larvae amounted to 18 per square foot and emergence was reduced to 52 beetles. This indicates that the clerids are capable of destroying two-thirds of the brood.

An important larval habit of the black-bellied clerid is its tendency to move freely through or over the bark and migrate when conditions become unfavorable. In 1928 Person (*U244*) made a study of this migration in infested trees that were felled so as to expose the top of the log to solar heat. He found that the clerids moved away from the top of the log where temperatures were sufficiently high to kill the western pine beetle and concentrated on the shaded sides and bottom of the log.

This habit suggested the possibility of building up the ratio of clerids to western pine beetle populations by falling the infested summer brood trees, leaving the bark on the log, and turning it at intervals so that most of the bark beetle broods would be killed by solar heat. This treatment, it was thought, would preserve the clerids by giving them an opportunity to migrate to the shaded sides of the log. Following up this idea, Person (*U246*) carried out a series of experiments during the summer of 1929 by falling infested trees and leaving the unpeeled log exposed to the sun. He found that:

1. Bark temperatures fatal to advanced broods of the western pine beetle are reached in unpeeled logs exposed to direct sunlight on moderately level or southerly slopes when air temperatures over 90° F. are reached; and
2. No evidence of mortality among clerids was found even when the highest bark temperatures were reached.

The next year Person (*U248*) uncovered further information limiting the practical application of this proposed control method. He concluded that it is applicable only to the summer period, when high temperatures prevail, and in fairly open stands where the topography is moderately level with few steep northerly exposures. The study was closed with Person's (*113*) published article.

The Red-Bellied Clerid (Enoclerus sphegeus (Fabr.))

The red-bellied clerid is commonly predaceous on the mountain pine beetle, the Black Hills beetle, and other bark beetles that develop in the inner bark. Its habits are similar to those of the black-bellied clerid. Person (*U240*) notes that it is "occasionally predaceous to western pine beetle adults, but never on the broods."

Miscellaneous Insect Predators

AULONIUM LONGUM Lec. (Family Colydiidae).—Keen (*U130*) found this beetle "abundantly in *D. brevicomis* infested trees" and assumed that it was predaceous. Person (*U240*) reported:

> Larvae have been found feeding on *D. brevicomis* larvae and pupae in a few instances, and this species may be considered occasionally predaceous. However, unsuccessful attempts to get either the larvae or the adults to feed on any of the stages of *D. brevicomis* . . . have convinced the writer that this insect is not typically predaceous, and in any case is of little importance in the natural control of the western pine beetle.

DERETAPHRUS OREGONENSIS Horn. (Family Colydiidae).—According to Person (U*240*) "this is a predaceous colydiid occasionally found with *D. brevicomis* but never reported as one of its predators." Keen (*62*) reports it as "predaceous on some of the Cerambycid and Buprestid larvae."

CUCUJUS FLAVIPES Fab. (Family Cucujidae).—This is a showy red beetle that is known to be predaceous in both the larval and adult stages. It is common in recently abandoned trees, but according to Person (*U240*) "is seldom associated with *D. brevicomis*. It is a common enemy of termites and secondary beetles."

PLATYSOMA PUNCTIGERUM Lec. (Family Histeridae).—An experiment by Struble (*125*) showed that this predaceous beetle would feed upon western pine beetle eggs, but the life history was not well synchronized with that of the western pine beetle. As a result there is considerable doubt as to its effectiveness as an egg predator.

PLEGADERUS NITIDUS Horn. (Family Histeridae).—Struble (*125*, *U293*) reports that this beetle feeds during both its larval and adult stages upon the eggs of the western pine beetle. Struble's studies present the only verified records of destruction of the eggs by insects. Yet the presence of other small predaceous beetles, diptera, and pseudoscorpions in the egg galleries has led to the suspicion that some of these may feed at times upon eggs of the western pine beetle.

OTHNIUS UMBROSUS Lec. (Family Othniidae).—Keen (*U130*) found this small gray beetle in great numbers in infested trees, and suspected it of being predaceous. Person (*U240*) reports that it "has never been reported as feeding on *D. brevicomis*. In the larval stage it is known to be predaceous on *Ips oregoni* broods."

CORTICEUS PARALLELUS (Melsh) (Family Tenebrionidae).—Keen (*U130*) reports "a few dead adults of *D. brevicomis* being eaten by these beetles." Person (*U240*) states that "they have never been reported as predaceous on any of the stages of *D. brevicomis*." Struble (*125*), found that "the adults as well as the larvae are phytophagus, feeding on fungi under the bark."

Aside from Coleoptera, other insects have been found preying upon the western pine beetle, although they are not considered important factors in control.

FORMICA HAEMORRHOIDALIS Emery (Hymenoptera).—Keen (*U130*) found these large red ants to be a serious nuisance in experimental cages where western pine beetles were emerging. "They grab the beetle with their mandibles, double under their abdomen and sting it, and then carry it away. As they are often seen running over infested trees, they probably render a great service in the control of the beetles." Person (*U240*) states that these red ants and also large black ants of the genus *Camponotus* "have frequently been known to capture western pine beetle adults and carry them away to their nests, and where abundant, they may be a factor in natural control."

RAPHIDIA OBLITA Hagen (Neuroptera).—Person (*U240*) was able to get "the large larvae of this insect to feed on small *D. brevicomis* larvae, but they were not able to feed on the larger larvae. They feed naturally on small dipterous larvae beneath the bark of infested trees. It is commonly associated with *D. brevicomis* in infested trees, but apparently is not normally predaceous on this bark beetle."

Mites

According to Rust (*117*) mites are important predators of bark beetle eggs. He observed their feeding habits on the eggs of the Oregon pine engraver and estimated that from 10 to 85 percent of the eggs were devoured. Mortality ranged from 52 percent in the first generation to 85 percent in the fifth generation, and varied from 10 to 25 percent in the intervening generations. But Rust also observed mites feeding on the eggs of the Douglas-fir beetle [*Dendroctonus pseudotsugae* (Hopk.)]; he attributed to mites a mortality of 62.5 percent of the total eggs deposited.

Although mites have not been recorded as feeding on the eggs of the western pine beetle, it is probable that they do. Mites have been frequently observed on the adult beetles and in the egg galleries, and it is to be expected that the role of their association with the beetles is similar to that with the engravers.

Certain soft-bodied mites (*Pediculoides* sp.) have been reported to feed on the larvae and pupae of the western pine beetle, especially when mite populations become established in rearing material. No studies seem to have been made, however, to determine the effectiveness of mites in causing mortality of beetle broods. Rust (*117*) refers to the relation of mites to larval mortality of bark beetles and states that "it is possible that mites are the most important biological agent in the destruction of various species of bark beetles," but he does not specifically attribute mortality of western pine beetle larval broods to mites.

Nemic Parasites

Certain nematodes associated with the mountain pine beetle have been described by Steiner (*123*) and Thorne (*133*), but so far no studies have been reported of nemic parasites associated with the western pine beetle. Undoubtedly a number of species exist which have not as yet been recognized.

Steiner suggested that "some of the nemas may prove of value in the control of beetles by acting as disease carriers and as consumers of weak or even healthy beetles and their eggs." He described three species of nematodes associated with the mountain pine beetle and suggested that two species of the genus *Aphelenchoides* may be true parasites, but this relationship was not fully determined. Thorne described nine more species of nemic parasites associated with the mountain pine beetle, but did not determine that any of these were primary parasites.

Fungi

An undetermined white fungus occurring in the inner bark of infested trees has been found to cause mortality of the young larval stages of the western pine beetle. It may be an important factor in natural control. When an epidemic on Modoc National Forest went into a decline, Salman and Bongberg (*U283*) reported:

> Early in the spring of 1935, a fungus having a white mycelium was found to be abundant in the galleries of broods that had overwintered in the younger larval stages. Observations made while counting broods in bark samples revealed that a considerable portion of the brood apparently had been killed by the action of the fungus. A study of the population figures secured from periodical brood counts showed in general that in trees in which the fungus was found the mortality in larval stages was higher than the average.

A green mold also develops in the inner bark under favorable moisture conditions, and has been considered detrimental to the broods. It has been found most commonly in connection with rearing experiments in the laboratory. According to Beal (*U6*)

> . . . a green fungus, identified by Wagener as a *Pencillium* was particularly abundant in the larval galleries where the brood had failed. Whether this fungus plays a part in the death of the larvae or whether it merely finds good growing conditions on the bodies of dead larvae is not known. However, because of the general saprophytic nature of this group of fungi, it is believed to be of little importance in the death of the insects.

Bacteria

The possibility of bacterial diseases becoming a factor in the control of the western pine beetle was mentioned by Person (*U240*). However, no evidence has been produced to indicate that anything in the nature of a wilt disease occurs in bark beetle larvae, and this lack of evidence lends support to the assumption that bacteria are not a factor in the natural control of the western pine beetle.

Viruses

No virus infection has been found associated with the western pine beetle. According to Steinhaus (*124, p. 496*),"No sound well-authenticated report of a virus infection in a coleopterous insect has yet been made."

FACTORS CAUSING MORTALITY DURING THE FLIGHT PERIOD

From the time beetles leave the protection of the bark—during flight and until they become established as parents in newly attacked trees—they are subjected to many chances of premature death. Beetle mortality during the flight period is often greater than it is during the developmental period in the host tree. Of an average of 92 beetles emerging to 25 attacking per square foot, the normal flight mortality is 73 percent even if the number of trees from one generation to the next remains the same. If there is also a reduction in number of trees attacked between generations, the flight mortality is even greater.

Mortality during the flight period has not received much study owing to the difficulty of tracing beetles after they have left a tree. Predators are known to affect mortality during this period, particularly certain beetles and birds. Unfavorable weather conditions and the resistance of host trees also are suspected of being dominant factors.

Predators

Patterson (*U220*) called attention to soft-billed, insect-feeding birds, such as vireos, creepers, nuthatches, and flycatchers, as possibly being effective feeders on bark beetles during flight, but there is little evidence to show that they actually are. Predation by birds has not been investigated for the western pine beetle, but it has for the mountain pine beetle. In 1928 and 1929, Rust (*U252*) collected specimens of five different species of insectivorous birds while the beetles were flying in a heavily infested area near Sula, Mont. From stomach examinations, he concluded that "insectivorous birds destroy many *D. monticolae* adults during their flight period." Of the five species examined, the most important were nighthawks, Alpine three-toed woodpeckers, and the Rocky Mountain hairy woodpecker. Since it is not to be expected that these birds discriminate between such closely allied insects as the western pine beetle and the mountain pine beetle, a certain number of the former are undoubtedly captured in flight in areas inhabited by nighthawks and birds of similar feeding habits.

Some predaceous beetles capture western pine beetle adults when they are leaving brood trees or landing on trees to be attacked. These include the blue-green trogositid, the black-bellied clerid, and possibly others. Predaceous insects may destroy a large number of adult beetles during the flight period.

Unfavorable Weather

Unseasonable weather conditions, such as high winds or heavy rains, may destroy a high percentage of beetles in flight. Since the beetles emerge only under favorable temperature conditions, it is probably unusual for them to be caught in flight by sudden unseasonable weather changes; yet it can happen.

Resistance of the Host Trees

The western pine beetle is usually unable to make successful attacks on thrifty, fast-growing host trees. Therefore a great many beetles must be lost during the flight period in an unsuccessful search for suitable trees to attack.

INSECTS ASSOCIATED WITH THE WESTERN PINE BEETLE IN ATTACKS UPON THE LIVING TREE

The Insect Fauna of Beetle-Killed Trees

Caging experiments have shown that the western pine beetle is quite capable of killing a tree without the aid of other insects. In the great majority of infested trees, however, it is joined by other cambium feeders. These associated insects usually occupy a smaller bark area than the western pine beetle, but they attack the living tissues of the inner bark, sometimes in advance of attack by the pine beetle.

Associated insects may have special significance in that they either weaken a tree so that it becomes attractive to the western pine beetle or are capable of taking advantage of a weakened condition that has already developed from other causes. Thus, an infestation of certain associated insects, such as engraver beetles, often acts as a fuse for a serious western pine beetle epidemic. Consequently, when timber losses from western pine beetle activity are discussed, they include the activity of all associated species commonly found in killed trees as part of the western pine beetle complex because the relationship between these species and the western pine beetle may yield clues to the increase and decrease of western pine beetle infestations.

Habits and Roles of Associated Species

The Mountain Pine Beetle (Dendroctonus monticolae Hopk.)

The mountain pine beetle, a primary enemy of lodgepole pine, sugar pine, western white pine, and pole stands of ponderosa pine also occurs in association with the western pine beetle in larger ponderosa pine (*48*). Evenden, Bedard, and Struble (*34*) have presented the more important biological information concerning this beetle and listed ponderosa pine as one of its hosts. They state, however, that "In California the beetle selects sugar pine in preference to ponderosa pine." They do not discuss the association of the mountain pine beetle with western pine beetle infestations.

Struble (*U304*) described its role as an associated insect in California as follows:

> The mountain pine beetle occurs frequently in association with the western pine beetle in ponderosa pine. Sometimes its attacks are mixed in with western pine beetle infestations; sometimes it occurs as a fill-in species between portions of the hole which were unattacked by *D. brevicomis*. The mountain pine beetle is also

often found in association with flatheads, *Ips*, or a combined association with all these insects. Under some conditions, it is the dominant species comprising the total infestation in a given tree. In general, the infestations of this bark beetle are regarded as of less consequence in ponderosa pine than other primary species associated with the western pine beetle.

In their composition studies, Salman (*U271*) and Johnson (*U111*, *U115*) found that the role of the mountain pine beetle in mixed infestations with the western pine beetle was largely secondary.

Struble (*U209*) found some striking differences in behavior of the mountain pine beetle between eastside and westside pine types. In the eastside type, 19 percent of 278 trees contained mountain pine beetle infestations which occurred mainly near the basal part of the bole; in contrast, in the westside type 65 percent of 100 trees contained mountain pine beetle infestations which occurred mainly in the midbole. This difference in behavior is not easily explained. Struble suggested that the greater incidence of the beetle in westside stands is "the result of a much closer association with sugar pine which is the preferred host of the mountain pine beetle." Probably, centers of attack in sugar pine sometimes overflow to nearby ponderosa pine. Also, the moister westside conditions may be more favorable for this beetle's development than the more arid eastside.

The Red Turpentine Beetle (Dendroctonus valens Lec.)

The red turpentine beetle is probably the most common species of bark beetle found attacking practically all species of pine and spruce throughout North America. Hopkins (*44, p. 156*) recognized its common role and preferences when he stated:

> This species prefers to enter the bark of injured or dying trees or that of stumps and logs of those which have been felled, but often attacks the perfectly healthy bark on the base and roots of healthy, living trees. It is often exceedingly abundant in the stumps of felled trees where timber-cutting operations are on, in fire-scorched trees, and especially in the bark at the base of those killed by other species of *Dendroctonus*, or by lightning or storm, or otherwise injured and broken. It shows a decided preference for the bark on the base of pine trees and stumps, and is rarely common in the logs or prostrate trunks, even of pine.

Its attacks on standing trees seldom are more than 6 feet above the root collar, but may extend down the main roots for 15 feet or more.

This species is strongly attracted to stumps on recently cut-over areas, and to injured or weakened trees. Bongberg (*U24*) found red turpentine beetles attacking stumps and an occasional green tree along with freshly cut stumps on Blacks Mountain Experimental Forest, and Johnson (*U118*) found that "the only attacks on standing trees in cut-over areas were on trees either injured by logging or those close to stumps or green logs."

This beetle has rarely been regarded as a primary tree-killing species in ponderosa pine, but whether it is one of the first to attack and weaken trees or follows the attack of other species has not been certain. In studying this species in relation to other species associated with the western pine beetle on Sierra National Forest in

1927, Struble (*U292*) concluded that "*D. valens* is a secondary insect and is rarely able to make successful attacks until the tree has been overcome by some other agency." He believed that the scent of fresh pitch tubes of the other species was influential in attracting the red turpentine beetle to the attacked trees. When in association with the western pine beetle, the California five-spined engraver, the mountain pine beetle, and flatheaded borers, the red turpentine beetle usually had the youngest broods; therefore it probably was the last or nearly the last insect to attack the trees.

On the other hand, in field studies in eastern Oregon it was found that the red turpentine beetle had a definite tendency to initiate attacks on very high-risk trees; such trees were four times as susceptible to subsequent attack by the western pine beetle as the average tree in the stand. Johnson (*U119*) found it attacking both high- and low-risk trees at Blacks Mountain Experimental Forest, sometimes following attacks by borers or pine beetles but occasionally before any other insects.

Often the red turpentine beetle tries to attack apparently vigorous green trees, but if it is not supported by other insects attacking up the main bole, it is usually drowned out by pitch flow and fails to develop successful broods. Repeated attacks may weaken trees until they become susceptible to other bark beetles.

The evidence so far strongly supports the conclusion that the red turpentine beetle is a secondary species in its association with the western pine beetle. It prefers to attack stumps, injured, weakened, or decadent trees. In ponderosa pine it usually follows other bark beetles or borers by attacking the base and roots of killed trees. But frequently it attacks fire-injured, drought-weakened, or decadent pines before other species do, and by its work at the base renders the trees more susceptible to primary species. It is doubtful whether the red turpentine beetle can attack and kill a fully vigorous, healthy tree, without assistance from other primary species.

Brood development is slow: a single generation a year in northern California (*U119*), one and a partial second generation in the southern Sierras (*U292*), and probably two generations a year in the San Francisco bay area (*139*).

The red turpentine beetle can be controlled in park and shade trees by injecting orthodichlorobenzene, ethylene dichloride, or carbon disulfide into the tunnels (*U255*) or by cutting out the galleries of the beetle with a chisel and then coating the exposed wood with pruning paint (*28*).

The Oregon Pine Engraver (Ips oregonis (Eichh.))

The Oregon pine engraver is commonly associated with the western pine beetle in the interior ponderosa pine type. Although it breeds in windfalls, and occasionally in large standing trees in conjunction with attacks by the western pine beetle, it more commonly kills large patches of reproduction, trees of pole size, or the tops of older trees without association with the western pine beetle. Usually it attacks where the bark is thin, either on small trees, the tops of larger ones, or on the larger limbs. The attacks may either precede or follow an attack of western pine beetles on the main bole. They often represent a small part of an infestation found in the tops of trees attacked

and killed by the western pine beetle or in poles, quite independent of the western pine beetle. Its egg galleries may also occur in mixture with western pine beetles in the upper half of the bole under thicker bark. Much information concerning this species has accumulated in manuscript and progress reports, but little has been published.

Outbreaks have almost invariably followed windfalls (*93*, *141*), logging disturbance (*U137*, *U194*, *U9*, *U40*), slash due to road construction or pine thinnings (*U63*, *U234*, *U1*, *U2*), and drought years (*U93*).

Keen (*U134*) studied the seasonal history and habits of this species in the Ashland area of southern Oregon and reported 54 days from first attack on April 10 to first emergence on June 3. Although the generations were not closely followed, they indicated "one summer generation in newly felled logs, and an overwintering generation in the tops of mature or young trees."

Rust (*U256*), who studied the species intensively for three seasons in Idaho, found four generations produced annually with a fifth generation produced in the exceptionally long season of 1931. In the Black Hills of South Dakota, Baumhofer and Hauke (*U2*) found three generations with only two and a partial third generation produced in some years.

Buckhorn (*U40*) found that the main attack on slash in eastern Oregon usually occurred about the middle of April, and heavy emergence from slash occurred about the middle of June. General attack on reproduction and standing trees started early in July and continued during August and September. Rust (*U256*) found a minimum time of attack to emergence of 24 days, but the usual time was from 30 to 66 days.

One peculiarity of this beetle is the habit of the adults to congregate under the bark of small trees late in the summer and fall. There they feed on the inner phloem and reduce it to powder. Another striking habit is that of the adults to overwinter in great numbers in bark crevices at the base of trees, in forest duff, and in egg galleries of the western pine beetle. Keen's note (*67*) was the first published information on this hibernating habit. The extent to which engraver populations overwinter in this way was effectively demonstrated by caging experiments conducted by Buckhorn (*U37*, *U38*, *U39*) in eastern Oregon.

The Oregon pine engraver is present every year, but outbreaks occur in certain "*Ips* years" and, as shown by Buckhorn (*U40*), seem to be tied in to precipitation deficiencies. Outbreaks are sporadic in occurrence and usually take smaller trees than are attractive to the western pine beetle. Therefore its association with the western pine beetle is usually of minor importance.

The California Five-Spined Engraver (Ips confusus Lec.)

Some of the earliest work in California was concerned with the habits, seasonal history, and control of the five-spined engraver. The first observations were made near Pyramid Ranger Station, above Placerville, Calif., in 1906. Intermittent studies and notes by several forest entomologists have accumulated a good deal of information

on this species. Those who made special studies include Keen (*U128*) at Ashland, Oreg.; Herbert (*U99*) at Placerville, Calif.; Miller (*U181*) on the Kaweah River; Furniss (*U65*) near North Fork, Calif.; and Salman (*U271*) in connection with the composition studies. In 1945, Miller (*U201*) summarized the notes and reports on this species in the Berkeley files. Further work was undertaken on the biology, ecology, and control of this species from 1946 to 1950 by Struble (*U307*, *U308*, *U309*, *U310*, *U311*), and Hall (*U87*, *U88*, *U89*). Results of this most recent work together with information from earlier studies have been published (*129*).

Hosts recorded in Berkeley Laboratory collections include 10 native pines: *Pinus attenuata*, *P. balfouriana*, *P. coulteri*, *P. jeffreyi*, *P. lambertiana*, *P. monophylla*, *P. monticola*, *P. ponderosa*, *P. radiata*, *and P. sabiniana.* Out of the 158 note entries, 114 apply to ponderosa pine, which is obviously one of the preferred hosts. The notes show the beetle distributed through the westside pine types from the Rogue River in Oregon, to the Laguna Mountains in San Diego County, Calif. It is significant that these notes contain no record of the California five-spined engraver from any areas east of the Cascade Mountains or the northern Sierra Nevada. Doane (*29*) found it in Monterey pine near Palo Alto, Calif., for the first time in 1921, apparently brought in with slabs of ponderosa pine wood.

The biology, seasonal history, and habits of the California five-spined engraver can be broadly sketched from the available information. All reports agree that for the most part, broods carry through the winter in standing trees attacked the preceding fall, and that these broods are made up mainly of new adults with some advanced larvae and pupae. The development of generations through the active season depends upon latitude and elevation, and may vary from two to four, with sometimes a partial fifth.

Infestations appear to be similar to those of the Oregon pine engraver. Under endemic conditions both engravers maintain themselves in recently felled logs, tops, and limbs. These infestations may be followed by localized attacks on nearby standing green trees. When outbreaks of the California five-spined engraver occur, a somewhat larger class of poles and young trees are attacked and killed. An immense amount of damage may spread rapidly over large areas. Extensive outbreaks have usually been short lived and often are associated with or followed by the western pine beetle. The western pine beetle breeds in the green boles of the top-killed trees and carries on the momentum of the epidemic for several years even after the engravers have subsided.

"*Ips* years" have been recorded as follows: Sierra National Forest, 1912–13; Placerville, 1914–16; Ashland, Oreg., area, 1915–16; west slope of the Sierra Nevada, 1929–32; northern California, 1938 (*U277*); the Burney and west slope Sierra areas, 1944–45. In southern California outbreaks have occurred every few years since observations were first made on the Julian area in 1915; the latest outbreaks started on this area in 1945 and were reported by Engen (*U57*, *U58*).

The tie between western pine beetle epidemics and preliminary engraver outbreaks was not well established in early records. Field-workers generally recognized that some western pine beetle epidemics

were preceded by widespread tree-killing and top-killing by engraver beetles before the western pine beetle became the dominant insect. This applies especially to outbreaks near the Rogue River (1914–17) and in the westside Sierra (1912–17 and 1929–33). These were areas in the westside pine types, where the California five-spined engraver was the species concerned. There is no evidence of a similar sequence in the eastside pine types, where the Oregon pine engraver is involved.

In the outbreaks, investigators concentrated on the biology and ecology of engraver beetles. They made no special effort to show quantitatively the buildup of western pine beetle after engraver infestations. Nevertheless, some evidence was obtained (table 2). Though only estimates, the ratios of the two insects in these areas serve to show the change from engravers to a predominantly western pine beetle population on most areas.

In the Burney area no serious epidemic of the western pine beetle occurred, but in the endemic infestation that followed the outbreak, the western pine beetle became the dominant insect. In the Cobb Mountain area there was an apparent reversal of the population ratio in midseason the first year after the outbreak. In the Sierra area the western pine beetle apparently required two seasons to reach its full momentum, while at Julian it required four. There is no evidence that control work or natural control factors against engravers had much effect in preventing the buildup of western pine beetle.

Epidemics of engraver beetles have been attributed to varied causes. Nearly all observers have assumed that the attacks in groups of standing green poles and the tops of living trees stemmed from populations built up by breeding in tops and logs of freshly felled trees, or in injured and dying standing trees. Several conditions are considered as contributing causes for outbreaks: Windfalls, snowbreak, slash created by wood cutting, logging operations, thinnings, road and reservoir development, flooding of pole stands, drought, suppression of tree growth, and the effects of fire injury.

TABLE 2.—*Estimated ratio of Ips to Dendroctonus brevicomis during origin of outbreak and subsequent years, California*

Area	During origin of outbreak	Following outbreak	
Burney	General outbreak started in 1943 and continued in 1944. Composed of: *Ips*—approx. 75%. *D.b.*—approx. 25%. Control—spring 1945.	*Season of 1945.*—Total infestation greatly reduced. Composed of: *Ips*—20%. *D.b.*—80%. Control, spring 1946.	*Season of 1946.*—Endemic infestations, some local outbreaks. *Ips*—10%. *D.b.*—90%.
Cobb Mt	Heavy general outbreak in fall 1948. *Ips*—90%. *D.b.*—10%. Control—spring 1949.	*Season of 1949.*—Spring period *Ips* bred up in snowbreak and attacked living trees. *Ips*—90%. *D.b.*—10%.	*Season of 1949.*—Late fall period, heavy infestation in large trees. *Ips*—50%. *D.b.*—50%.
Sierra (Mariposa and King's River).	Heavy *Ips* outbreaks around cutting areas during season of 1947. *Ips*—90%. *D.b.*—10%. No control.	*Season of 1948.*—Infestation greatly reduced. Composed of: *Ips*—80%. *D.b.*—20%.	*Season of 1949.*—Epidemic conditions. *Ips*—10%. *D.b.*—90%.
Julian and Cuyamaca, southern California.	*Ips* outbreak started in 1945, discovered in 1946; control in 1947–48. *Ips*—90%. *D.b.*—10%.	*Season of 1948.*—Epidemic reduced; control continued. *Ips*—70%. *D.b.*—30%.	*Season of 1949.*—*Ips* epidemic greatly reduced. *D.b.* population increasing. *Ips*—10%. *D.b.*—90%.

Some of these conditions seem plausible explanations for specific outbreaks, but no case can be said to have been conclusively proved. Several factors have been involved in every situation that has preceded an outbreak of the California five-spined engraver. Of these factors, the influence of precipitation and temperature have received special attention in studies since 1945.

Precipitation

Precipitation deficiencies were found to be associated with both recent and older epidemics of engraver beetles in California. Hall (*U89*) reviewed the known history and the available precipitation records of 12 epidemics extending from Ashland, Oreg., to Julian, Calif. For most of these outbreaks, precipitation deficiencies in the late winter and spring had preceded attacks in living trees during the late summer and fall. The precipitation pattern arrived at by plotting the arithmetical accumulation of departure from the monthly means developed a certain character by the early part of May, after which there was little change from the seasonal trend.

When the cumulative precipitation deficiency from January to June reached a point as low as 75 percent of normal, outbreaks usually occurred in the late summer and fall. Conversely, above-normal precipitation during this period usually coincided with very low or negligible damage by engraver beetles during the late season. In the Burney area, soil moisture was found to follow the precipitation trend and showed pretty much the same relationship to damage.

Temperature

In northern California, Hall (*U88*) reported marked differences between the seasons of 1947 and 1948 in the intensity of engraver beetle infestations, and attributed these differences to variations in precipitation and temperatures.

The year 1947 was one of heavy engraver beetle damage in the lower westside pine types. This season was characterized by seasonal precipitation well below normal, soil moisture well below normal during most of the growing season, and by air temperatures well above normal during most of the growing season. The season of 1948 was one of very light damage except in a few local areas. Seasonal precipitation and soil moisture were well above normal for the entire growing season, and air temperatures below normal through most of the season.

Hall (*U88*) estimated that the low temperatures in 1948 slowed down the development of engraver beetle broods to the extent that only 2½ generations were produced, against 3½ generations in 1947.

In the central Sierra, Struble (*U310*) found practically the same differences in number of generations between these two seasons. In the Julian area in southern California, however, Engen (*U58*) recorded prolonged seasonal activity in 1948. He estimated that four complete generations and a partial fifth were completed between April 14 and November 15. Some attacks of the first generation were noted in January and February 1948, but the brood development of these early attacks was very slow because of low temperatures before April.

Differences in Responses of Ips and Dendroctonus brevicomis to Climatic Influences

All investigators agree that a combination of subnormal seasonal precipitation and soil moisture, and above normal air temperatures during the growing period, sets up conditions highly favorable to engraver beetle activity and the prospect for outbreaks in living pine stands. Western pine beetle populations apparently respond similarly, but at a much slower rate: epidemics correlate well with cumulative deficiencies in precipitation extending over more than one season. Engraver beetle outbreaks, however, usually appear during the first season of drought. This point may explain the slower increase of western pine beetle populations.

Practically all engraver beetle epidemics have reached their peak in one or two seasons and have subsided as suddenly as they developed. Why this sudden decline occurs is as difficult to learn as the causes for a rapid increase. Only two explanations have been offered: "Lack of wind-blown material or other suitable material for the development of the first seasonal generation" (*U128*); and failure (from unknown causes) of overwintering broods to develop successfully in top-killed trees in the fall (*U65*). Although the ecological factors favorable to an increase in engraver populations appear favorable to western pine beetle increases, the natural control factors that bring about sudden declines in engravers apparently do not work so rapidly on western pine beetle epidemics. Hence these epidemics increase after the engraver outbreak has passed out of existence.

Direct Control

Direct control of the engravers has largely been considered incidental to the control of the western pine beetle in commercial pine stands. The policy seems to have been based on the expectation that the engraver infestation would die down quickly and that the important thing was to prevent the buildup of western pine beetle populations in trees injured by engravers. Miller (*U201*) stated that:

> The general policy regarding *Ips* on all direct control projects since 1920 has been to treat this infestation only when it could be included with the treatment of *D. brevicomis* and *D. monticolae* infestations, except on parks, recreational areas and other conditions where the character of the damage caused by *Ips* was considered to be a serious threat to tree cover values; in the latter case, the effort has been made to eradicate all *Ips* infestation in the control area.

Direct-control methods have consisted mainly of the cut-peel-burn technique, or in groups of pole trees, cutting and burning the trees in piles without peeling.

Indirect control has been practiced by forest management agencies through measures to prevent the slash conditions that provide breeding grounds for engravers. The measures include specific requirements for slash disposal on sporadic cuttings, such as right-of-way clearings and other operations that create a considerable concentration of slash for a short period. Continuous logging operations

have usually been excluded from special requirements because it was assumed that the constant supply of fresh slash under continued logging provided ample material to absorb surplus engraver beetle populations.

The Large Western Pine Engraver (Ips emarginatus Lec.)

This species is a common associated insect, but very little work has been done on its biology. Keen observed on the Ashland area in 1916 that ". . . there are at least two generations, one developing during the summer and another passing through the winter" (*U134*). Flight and new attacks were observed in May and June and again in August and September. The species overwinters as adults, eggs, and small larvae.

According to Salman (*U271*), the large western pine engraver is of relatively minor importance, usually occurring in association with other species, often following after them, and attacking in patches and strips left by other beetles on the middle and lower bole. In 1933 on Lassen National Forest, he found this species competing with the western pine beetle by following in, cleaning out, and widening the western pine beetle galleries. Many of the younger stages of western pine beetle broods were thus destroyed.

It is often associated with the mountain pine beetle in ponderosa pines of small diameter but is definitely a secondary species. Apparently it never becomes aggressive or is found attacking and killing tops or young trees as do the Oregon pine and California five-spined engravers.

The Flatheaded Borers (Buprestidae)

Although some of the flatheaded borers are cambium or phloem feeders, these insects are strikingly different from the scolytids in habits of attack and development. Eggs are laid in crevices of bark. Only the larvae penetrate into the phloem area, where they make flat tortuous mines packed with concentric layers of frass. Pupation occurs in cells in bark or outer wood.

The species most frequently found in the bark of ponderosa pine associated with the western pine beetle are the pine flatheaded borer (*Melanophila gentilis* Lec.) and the California flatheaded borer (*M. californica* VanD.).

Melanophila gentilis Lec.

The adult pine flatheaded borers are bluish green in color and 13 mm. long. Burke (*14*) records this species as mining the bark and outer wood of normal, injured, dying, and dead ponderosa pine, Jeffrey pine, and sugar pine throughout the Pacific States and Rocky Mountain region. Keen (*U134*) noted these flatheaded borers killing trees on the Ashland area from 1915 to 1917, but kept no consecutive records of their development. The species was considered to be the pine flatheaded borer, and those attacking logs probably were, but the species found in standing trees was probably the California flatheaded borer, which was not described by Van Dyke until 1918.

Salman (*U271*) and Salman and Bongberg (*U284*) determined that "*M. gentilis* appears to be the species chiefly concerned in infestations of felled trees, logs, windfalls, injured trees and in secondary bole infestations in standing trees." The more primary infestation in standing trees was due to the California flatheaded borer.

West (*U330*) confirmed this appraisal of the secondary role of the pine flatheaded borer. He found that in common with the California flatheaded borer the adult pine flatheaded borer emerges and has an extended flight period in the late spring, during which it feeds on pine foliage before it becomes sexually mature. Eggs are deposited on the outer bark and the young larvae feed in the cambium and inner bark. From this point on, however, the habits of the two species differ significantly. The pine flatheaded borer develops only in felled green trees, windfalls, phloem of infested trees, cull logs, and slash, and completes its life cycle in 1 year. In contrast, the California flatheaded borer completes its development only when the young larvae spend at least 1 season in the living phloem and cambium and usually require from 2 to 4 years to complete the life cycle. Therefore West concluded that the secondary importance of the pine flatheaded borer had been established to the point of dropping the species from serious consideration as an important factor in association with western pine beetle attack.

Melanophila californica Van Dyke

The adult California flatheaded borers are brownish black on the dorsal surface, and greenish bronze below. Some specimens have two to six yellow spots on the wing covers. The length is from 7 to 11 mm. This species was not recognized until 1918 when Van Dyke separated it from the flatheaded fir borer (*M. drummondi* Kby.) and its other near relatives.

Burke (*14*) reported it mining the inner bark and outer wood of normal, injured, dying, and dead ponderosa pine, Jeffrey pine, digger pine, Coulter pine, Monterey pine, and knobcone pine in California, Oregon, and Idaho.

In 1935, Salman (*U271*) found from composition studies that the California flatheaded borer and not the pine flatheaded borer was responsible for the greater part of the flatheaded borer infestation, particularly in eastside stands, where in some areas and seasons the flatheaded borer damage was nearly equal in amount to that caused by the western pine beetle. In westside stands, flatheaded borer infestation was usually confined to smaller trees growing on poor sites and to top-killing, particularly in the follow-up of top damage by the California five-spined engraver.

The composition studies also showed that on the eastside the attack by the California flatheaded borer frequently occurred in the tops of slow-growing trees and was usually followed by attacks of the western pine beetle. It was assumed, therefore, that initial attack by this flatheaded borer was a primary factor in weakening trees and in producing those characters associated with high risk of pine beetle attack. This led to a series of studies on the biology and role of this flatheaded borer in eastside pine stands.

West (*146*, *U330*) found that adult California flatheaded borers emerged during May, June, and July and became sexually mature only after feeding on the needles of ponderosa or Jeffrey pine. They then laid eggs during June, July, and August on the outer bark of living trees. Upon hatching, the larvae worked into the cambium area and began feeding. These first larval mines were associated with wartlike scars formed by wood tissues laid down over the feeding injury. This peculiar phase of feeding, in which the tree continued to grow and the larva very slowly increased in size and widened its mine, was termed the *incipient stage*. It was found to persist from 1 to 4 years, depending on how long the tree continued to live and form scar tissues around the mine.

Once the tree ceased growing, the larva passed into the *fast growing stage*, in which it began feeding rapidly in the inner bark, completed its development, and pupated in the outer bark. This stage was usually completed within the same season that the larvae changed over from the incipient stage. As a rule the fast-growing stage overwintered as prepupal larvae in the outer bark and the following spring transformed to the new adults and emerged. A diagram of the seasonal and life history of this species as worked out by West is shown in figure 22.

In 1936 West (*U323*) made a thorough investigation of the biology of the California flatheaded borer. A field laboratory with insectary and rearing cages on Modoc National Forest was used to study all phases of the insect's behavior under control. The more significant points established were:

Needle feeding is a requisite of adult life.

Attempted forced attacks on green logs were definitely unsuccessful.

The life cycle of *M. californica* in northern California is generally longer than 1 year.

The length of time spent in the incipient larval stage depends on the condition of the host.

Many trees bear evidence of continued unsuccessful incipient attacks.

The growth from the incipient to the prepupal stage is very rapid.

In mixed stands of ponderosa and Jeffrey pine, the latter is apparently the preferred host.

West (*U322*) ran a short series of laboratory tests at Berkeley to determine the cold resistance of flatheaded borer larvae. These tests indicated appreciable mortality after several days' exposure between 14° and 0° F., and increasing mortality from 0° to −15°. West pointed out, however, that the results did not apply to field conditions since larvae used in the tests did not undergo the hardening process of fall weather.

West (*U325*) added to the knowledge of the species and verified previous results. The incipient stage was definitely established to last from 1 to 4 years. He found that:

> . . . the life cycle for the greater part of an emerging brood has been 2 or more years. Larval studies have shown that as many as 4 distinct ages of incipient larvae may be present in the same section of an infested bole, with the proportion of larvae

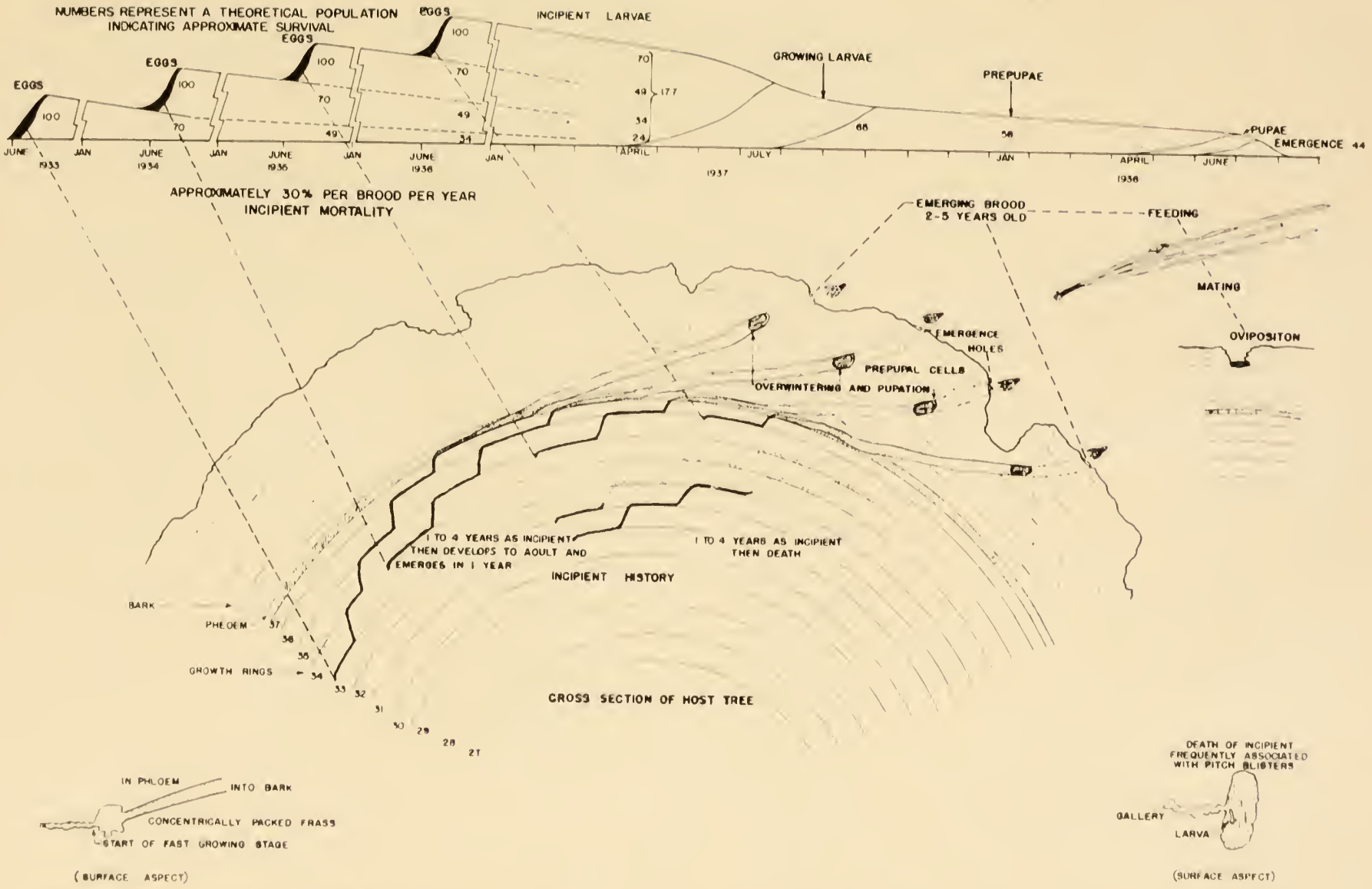

FIGURE 22.—Life cycle of a typical California flathead borer (*Melanophila californica*) mixed-age brood.

> of any one age to the total brood varying inversely with the age of the group . . . The physiological condition of the host determines the time when larvae leave the incipient stage to complete their development.

A period of feeding in living cambium, West found, is a requirement for successful development of California flatheaded borer larvae, and this habit requires a life cycle of at least 2 years; these are specific differences between the habits of this species and those of the pine flatheaded borer. A paper summarizing these studies was published in 1947 (*146*).

In 1941 Johnson (*U113*) rechecked West's studies. He found that "at times small larvae of the season may be able to develop into the fast growing condition and possibly to maturity without having spent a year in the green trees as incipients." The supporting data, however, were limited to one or possibly two trees out of many studied. Johnson also investigated the possibility that incipient larvae may go into the fast-growing stage, pupate, and change to adults in the same season without overwintering as mature larvae. He concluded "it may be possible that development from incipient to the adult can occur within a single growing season, although the data are inconclusive for this possibility." Johnson (*U117*) also found that in some atypical cases, emergence from the same piece of bark may occur during two seasons. However, such split emergence seems to be of infrequent occurrence.

Rust's (*U257*) rearing experiments at Coeur d'Alene, Idaho, 1939–42 also indicated the possibility that the California flatheaded borer may complete its life cycle in 1 year and that it may develop successfully in slash. These results, however, were not conclusive.

The capacity of this species to weaken trees and make them attractive to western pine beetle attack was considered to be due to the injury caused by the incipient mines in the cambium. West (*U324*) made a careful histological study of the nature of these mines to determine the type of injury they produce and their effect upon tree growth. He found that the healing over of the lesion was accompanied by formation of abnormal tissue and that resins infiltrated much of the tissue surrounding the scar.

It was suspected that this abnormal tissue and the resins could affect the tree's functions adversely by blocking conduction. To determine this point, Salman and Johnson (*U288*) studied the movement of water through and around the scars produced by incipient larval mines in living trees. A special staining technique showed the rate of flow of silver nitrate solutions through different wood layers. The wood material used was collected from living trees, and the solution was immediately injected through gravity pressure. The outer wood rings conducted the solution most readily, but the movement was retarded when flathead scars were present. They concluded that:

> . . . flathead scars seem to have a definite blocking effect upon solutions moving dynamically through scarred wood. This effect results in a reduction in the amount of wood available for rapid transport of the staining solution longitudinally through the wood. If the results of this study are applicable to living trees, the flathead scars may exercise a definite influence upon the tree by affecting the water relations.

Salman (*U279*) explored the effect of incipient scars upon the growth rate and the relation of these scars to risk in ponderosa pine on Modoc National Forest. He reached the following conclusions:

> The types of trees in which most of the loss has been recorded, i.e., high risk trees, are generally the slower growing ones.
>
> The slow growth rate is of recent origin and probably temporary, to be terminated by death or recovery.
>
> Incipient infestations tended to occur more often in the trees which subsequently died than they did in the stand as a whole.

Salman's data also showed that incipient infestations preceded death in 80 percent of the trees that were attacked by the western pine beetle. His results indicated that for this particular area the association of the California flatheaded borer with the western pine beetle was practically universal and that the presence of incipient larval mines is associated with, if not the cause of, recent suppression of growth rate.

Twig Beetles (Pityophthorus and Pityogenes)

Other beetles that at times appear to be associated with attacks by the western pine beetle are the tiny scolytids that breed in the thin bark of the extreme top, limbs, and twigs.

The most common species in this type of association belong to the genus *Pityophthorus*. Their activity is associated with the killing of the upper 2 to 10 feet of the crown. Sometimes pine engravers and the western pine beetle subsequently attack the main bole; more often no subsequent attack develops, and the tree survives with a small dead spike in the top. Because of the limited character of the attack, this type of injury has been termed "tip killing." It is sporadic, developing suddenly over wide areas one season and disappearing the next.

In 1935 and 1936, Salman (*120*) studied a tip-killing epidemic prevalent in several forested areas in northern California. He noted:

> The *Pityophthorus* infestations were widespread and occurred in markedly different environments. They were present in stands of varied composition, character, and general vigor. They were found in both virgin and cutover stands. The thriftiest trees seemed to be selected for infestation to a greater degree than the less thrifty trees.

In the absence of any other evident primary cause he attributed the damage to two species of *Pityophthorus*, *P. confinis* Lec. and *P. confertus* Sw., though these insects had not previously been known to cause such damage. He stated, ". . . it is possible that the trees had previously been weakened and their resistance to insect attack reduced by some other environmental factor. If such was the case, that factor could not be determined."

Wagener (*136*) showed that top dying of Coulter pine on an area in southern California was due to freezing injury when a sudden cold spell followed a period of warm weather and that top dying on ponderosa pines in northern California was probably due to the same cause. He stated:

> Similar freezing injury has been found in connection with top dying of ponderosa pine in northern California and may have

been the primary cause for earlier top kill in this species ascribed to *Pityophthorus* beetles. . . . Freezing is to be suspected as a cause when top dying appears early in the season and is confined to fully exposed tops of thrifty trees.

It has been found in general that western pine beetle attacks followed only when tip killing included more than the upper few feet of the top and was associated with some engraver beetle infestation.

Pityogenes carinulatus Lec. is sometimes found in trees infested by the western pine beetle. This scolytid attacks the lateral small branches and twigs of dying pines. No studies have been made of this association, but available records indicate that it is secondary. In all probability the scolytid is attracted to the tree after attacks by the western pine beetle or some other injury.

Defoliating Insects

Insects that feed on needles and thus defoliate pines may contribute to an attack of the western pine beetle. If defoliation is severe and rather sudden, the tendency is to stop transpiration and cause an accumulation of moisture, or "sour-sap," in the sapwood and phloem. This condition, decidedly unfavorable to bark beetle attack, has been noted after sudden defoliation by fire, needle-cast fungus, or insects. On the other hand, a slower, more progressive type of defoliation may cause a gradual suppression of growth and reduced tree vigor which will make trees susceptible to beetle attack. Two insects that feed on pine foliage have been found related to western pine beetle outbreaks in this way.

According to Webb (*144*), Hopkins found the western pine beetle on June 6, 1899, at Cedar Mountain, Idaho "in the bark of pine trees which had been defoliated the previous year by the caterpillars of the pine butterfly (*Neophasia menapia* Feld.). He found also that this beetle was quite intimately associated with the destruction of a large amount of timber only partly defoliated by the caterpillars."

Evenden (*32*) recorded an infestation of western pine beetle following defoliation by the pine butterfly near Spokane, Wash., in 1922–23. On a plot study, 26 percent of the defoliated trees died within 13 years after defoliation. More than half of the trees that died were attacked by the western pine beetle; the remainder died from the effects of defoliation alone.

The effects of defoliation by the Pandora moth (*Coloradia pandora* Blake) on Klamath Indian Reservation were studied by Patterson (*107*) after an epidemic in 1918–25. This moth defoliates the trees only on alternate years and does not destroy the terminal buds; as a result, most of the trees survive the effects of the defoliation alone. However, Patterson states:

> The damage caused by bark-beetle attacks in stands of pine defoliated by the Pandora moth has been far greater than the primary damage of the defoliator. Infestations of *Dendroctonus brevicomis* and *D. monticolae* have shown an abnormal increase in the defoliated areas studied. These infestations were of far greater intensity than were contemporary infestations in stands

adjoining the defoliated areas, and beetle attacks upon defoliated trees were always fatal.

Scale Insects

Several species of the genus *Matsucoccus* form lesions in twigs, resulting in a sudden killing of individual twigs and small limbs known as "flagging." This capacity has been recognized since 1934. The injury thins and deteriorates the crown, and hence may contribute to bark beetle attack.

The first species of this group to be studied intensively was *Matsucoccus vexillorum* Morrison in connection with a "twig blight" in ponderosa pine through the southwest. The injury caused by this species, however, was not found to be conducive to bark beetle attacks.

Later McKenzie (*U174*) found that another species, *Matsucoccus bisetosus* Morrison produced lesions and resining in the axils of the twigs of ponderosa and Jeffrey pines which resulted in deterioration of the crown: this deterioration was much like the characteristics of "high-risk" trees, which are known to be susceptible to western pine beetle attack. McKenzie (*88*) pointed out that "this scale insect may be one of the important factors in the decadence of mature ponderosa pine and Jeffrey pine forests."

The role of *Matsucoccus* scale in the decadence of crowns of ponderosa and Jeffrey pine was studied in 1940 and was first reported upon by Johnson (*U110*). This study consisted primarily of "a survey of the distribution of *Matsucoccus* populations in (a) the crowns of Risk I and Risk IV ponderosa pine trees, and (b) in unhealthy areas of crowns." The survey was supplemented by life history studies and by tests to determine the effect of injuries produced by the scale on conductive properties of twig stems. A summary of this study prepared by McKenzie (*U175*) in 1942 pointed out that:

> . . . according to the data . . . as to the number of scales per square inch on the stems of low and high risk trees, there does not seem to be any particular significance in the *Matsucoccus* population in different parts of the crown. On the other hand if the extent of resining in the axils of the twigs from these trees is considered, the heavy axil resining does appear to be more prevalent on high risk trees than it does on those of low risk.

The scale study in general was inconclusive in establishing any relation between scale infestation and subsequent attack by the western pine beetle.

Needle-infesting scales such as *Phenacaspis pinifoliae* (Fitch) and *Aspidiotus californicus* (Colm.) at times cause defoliation and stunting of needle growth of ponderosa pines in restricted localities. Although no comprehensive studies have been made, observations by western forest entomologists tend to the conclusion that these infestations have no bearing upon western pine beetle attack. One area near Susanville, Calif., is recorded where an infestation of these two scales stunted the growth of a stand of ponderosa poles from 1922 to 1934. When these trees finally died, they were attacked only by flatheaded borers and not by western pine beetles.

Aphids

Aphids have been considered a possible factor in bringing about the deterioration of pines and their susceptibility to bark beetle attack. However, no evidence has been produced to support this assumption. West (*U321*) studied a heavy aphid infestation on ponderosa pine near Prescott, Ariz. His report discusses the injury to the stems caused by the feeding of these sucking insects, but establishes no relation to susceptibility of the trees to bark beetle attack.

Resin Midge (Retinodiplosis inopis (O.S.))

Resin midges kill twigs and stunt and deform small branches of ponderosa pine. Although this type of injury deteriorates the crowns of heavily attacked trees, it has not proved inducive to attack by bark beetles. The resin midge restricts its attack to young trees and to lower limbs of larger trees. As a result the injury probably has little effect on the vigor of the larger trees usually selected by pine beetles.

Composition Studies of Mixed Infestations

Common Infestation Types

Attacks of associated cambium-feeding insects are distributed on the main bole of an infested tree in many varied patterns, depending on species and the timing of attacks. When infested bark surface is mapped according to distribution of insect species, the trees can usually be grouped into a few recognizable infestation types. The types may vary in composition between areas and between seasons in the same area. However, a few standard patterns of attack are usually found in any infested area. The five more common infestation types are illustrated in figure 23. Type 1, consisting solely of western pine beetles, is usually less frequent than types 2 to 5; however, it is the most common type during epidemic periods.

At an early date investigators noted the varying composition of infestation in beetle-killed trees and wondered as to its significance. Questions arose as to how important certain combinations of beetles were, and whether or not some of the other species were more primary in killing trees than the western pine beetle.

Types Found in Early Studies, 1912–18

The association of western pine beetles with other insect species was first noted and studied in the first western pine beetle control projects on Klamath National Forest in 1912. On the Craggy Mountain area, Burke (*U42*) found that pure infestations of the western pine beetle occurred in only 16 percent of 514 treated trees, the flatheaded borer (*Melanophila* sp.) in 22 percent, and the mountain pine beetle in 2 percent; thus unmixed infestations killed 40 percent of the trees. Sixty percent of the trees contained mixed infestations: 33 percent western pine beetle and flatheaded borer; 14 percent mountain pine beetle and flatheaded borer; 10 percent

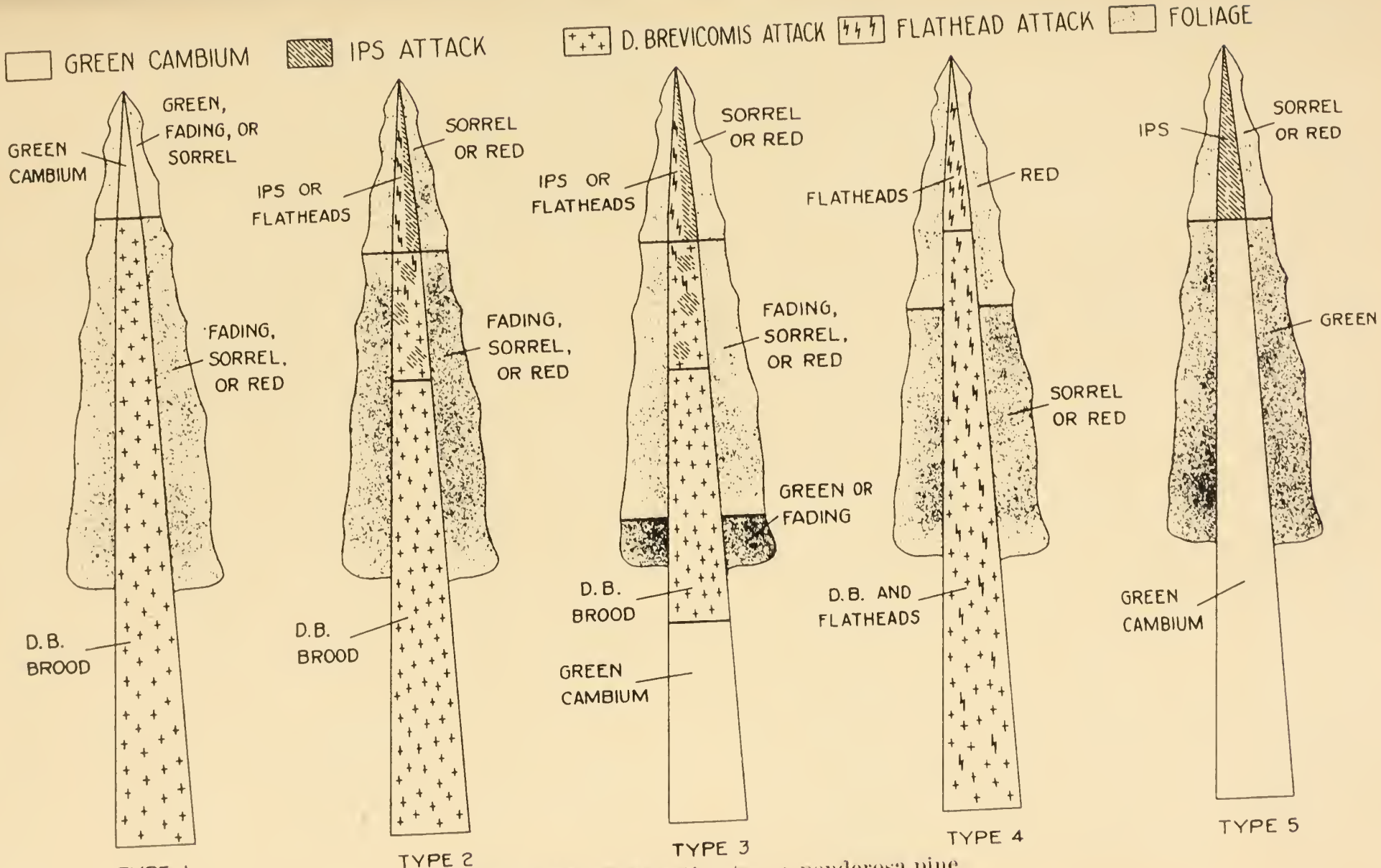

FIGURE 23.—Infestation types, ponderosa pine.

western pine beetle, mountain pine beetle, and flatheaded borer; and 3 percent western pine beetle and mountain pine beetle. In all, the western pine beetle occurred in 62 percent of the trees, as compared with 79 percent for the flatheaded borer and 29 percent for the mountain pine beetle.

Near Ashland, Oreg., Keen (*U133*) analyzed an infestation that developed from a top-killing epidemic starting in 1914. He recognized the mixed character of most of this infestation and tabulated the order and abundance of the various combinations of species found year to year. He designated as "primary" the insect considered responsible for the final death of the tree. For the 3-year period 1914–16 "*Ips* attack preceded *D. brevicomis* attack in 96 percent of the total trees killed (578)." But the final death of the tree was due to the western pine beetle in 49.5 percent of the cases, to the California five-spined engraver in 39.5 percent, to the mountain pine beetle in 8.8 percent, to flatheaded borers in 1.6 percent, and to emarginate ips in 0.6 percent. In trees killed primarily by the western pine beetle, various combinations of mountain pine beetle, red turpentine beetle, California five-spined engraver, emarginate ips, and flatheaded borers were noted as secondary.

Mixed infestations in the southern Sierra westside region of California were studied by Miller (*U180*) on control projects carried out on Sequoia National Park in 1918. He grouped 87 ponderosa pines, felled on the Kaweah Project in spring control work, according to the primary insect as recognized in the first examination by spotters, as follows:

	Trees (number)
Dendroctonus brevicomis primary	71
D. monticolae primary	6
Unknown (base green)	10
Total	87

The infestation that was found by examination of bark on the entire bole after the trees were felled was as follows:

	Trees (number)
D. brevicomis only	43
D. monticolae only	6
Ips confusus and *Ips oregoni*	4
D.b. associated with *D.m.*, and *Ips* in tops	28
Top-kill trees that would have survived if not felled (*Ips*)	6
Total	87

This comparison brought out the point that for this area and type of infestation the spotters' basal examination by no means gave a reliable index to the species of insects that attack the main bole of a tree.

The Devil's Garden Study, 1928–34

Since the typical composition of undisturbed infestations was known, the question arose as to whether control work would materially change the composition pattern. An opportunity to study this question was afforded by the Devil's Garden Extermination Experiment where all infested trees were treated from the spring of

1929 up to and including the 1931 overwintering generation. Records were maintained of the amount of bark surface infested by six species of associated insects, including western pine beetle, mountain pine beetle, red turpentine beetle, Oregon pine engraver, emarginate ips, and flatheaded borers. As the project progressed, it soon became apparent that the relationships of these species were not static but changed from year to year.

The importance of the species associated with the western pine beetle is illustrated in figure 24. This illustration shows the percent of total bark surface infested by each species of insect during each successive generation, beginning with the overwintering-generation trees of 1928 and ending with the summer-generation trees of 1931. The relative occurrence of the six species changed with each succeeding generation. The most significant point developed by the study was that as the western pine beetle was reduced by intensive control work, the pine flatheaded borer increased and eventually became the dominating species. In the overwintering brood trees of 1931 (not shown in fig. 24), the flatheaded borer population occupied 69.0 percent of the infested bark surface and the western pine beetle but 11.1 percent. Other species occupied the remaining bark surface. The two species of *Ips* and the mountain pine beetle did not show any significant trends in infestation during the period of the study.

Types in the Southern Sierra Nevada, 1930–32

The mixture of insect species comprising the attack became an important consideration in determining control policy on the Sugar Pine Sale project, Sierra National Forest, in 1931. This project was undertaken to control a widespread epidemic of the western pine beetle. Heavy top-killing by engraver beetles preceded the main attack of the western pine beetle. In the execution of control, it was necessary to decide whether to treat the trees infested only by engraver beetles in the tops or by engraver beetles in combination with a very light infestation of the western pine beetle. Such top-killed trees stood a good chance of survival unless attacked in the main bole by the western pine beetle. Gustafson (*U76*) recognized six types in the 1931-32 overwintering infestation. These types, in the order of decreasing importance, were:

1. Dendroctonus brevicomis–Ips confusus.—Top was attacked by the California five-spined engraver, western pine beetle mixed with California five-spined engraver in the midbole, and unmixed western pine beetle in the lower bole. The California five-spined engraver had apparently started the first attacks in the top; often the base was green and unattacked for 10 to 20 feet up from the stump. Trees of this type made up the great bulk of the overwintering infestation.

2. Dendroctonus brevicomis–Melanophila–Ips.—Attacked by engraver beetles in the top, a mixture of all three species in the midbole, and western pine beetle in the lower bole.

3. Dendroctonus brevicomis–Melanophila.—Attacked by flatheaded borers in the top, a mixture of western pine beetle and flatheaded borers in the midbole, and western pine beetle in the lower bole.

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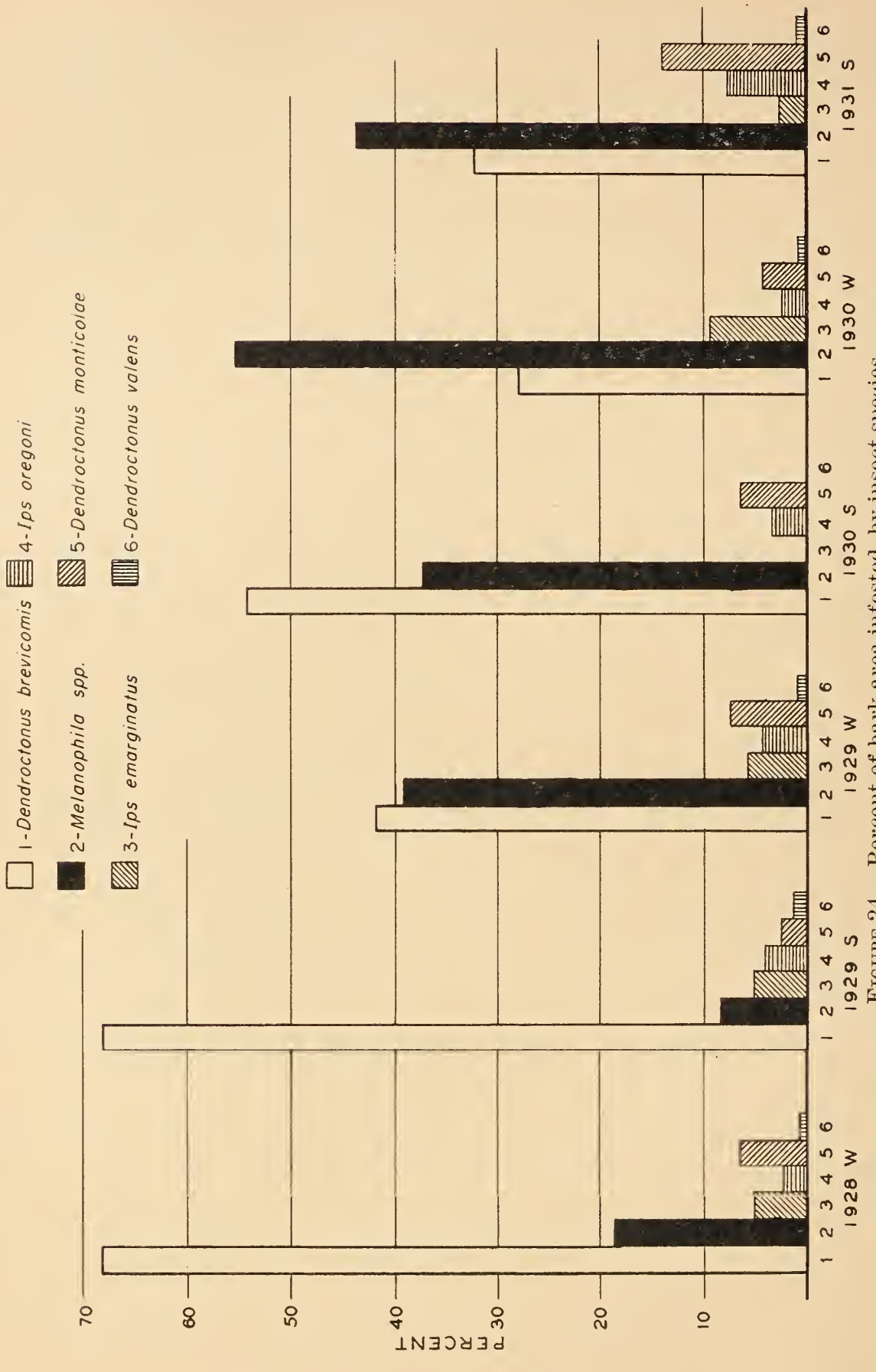

FIGURE 24.—Percent of bark area infested, by insect species.

4. Ips confusus.—About 25 to 45 feet of top attacked by this species, the entire lower bole unattacked. These trees were primarily top-kills with a good chance of survival if not attacked later by the western pine beetle.

5. Dendroctonus brevicomis.—Infestation of this beetle only occupied the main bole. The top, from the 6-inch diameter on up, was usually green and unattacked.

6. Melanophila californica.—The entire bole was attacked by this species. This type was confined almost entirely to Jeffrey pine.

The general practice adopted on the control operation was to leave top-killed trees (type 4) untreated if less than 50 percent of the upper bole had been attacked. Studies made on this area 2 years later showed that about 50 percent of the trees of this type had been attacked and killed by the western pine beetle but the remainder still survived as stag-tops.

Composition of this infestation changed very materially during the 1932 season, according to Furniss (*U65*). Early in the spring following control work, the engraver was reduced to a minor role: by fall it had almost completely disappeared. The flatheaded borer infestation, however, maintained its ratio in the composition with the western pine beetle and became relatively more important.

Regional Studies of Composition, 1931–35

Records from other control projects in the period 1931–35 emphasized the wide differences in abundance and behavior of insect species composing the different types of infestation. These records also emphasized that the differences are related to region of occurrence and to phases of the epidemic cycle. So abundant were associated insects in the earlier stages of an epidemic that some observers expressed considerable doubt as to the importance of the western pine beetle as a primary species.

To help resolve this doubt, Salman (*U271*) summarized records from various areas throughout the California region. This summary included records from 782 infested trees on 11 different areas extending from northeastern California to the southern Sierra region. The character and amount of infestation by different insect species were determined by sampling some 361,160 square feet of bark.

Salman listed seven insects as the more important ones found in association with the western pine beetle throughout the region: red turpentine beetle, mountain pine beetle, emarginate ips, Oregon pine engraver, California five-spined engraver, California flatheaded borer, and pine flatheaded borer. He found, however, that the western pine beetle alone "infested over 40 percent of the bark surface of trees included in the samples. It entered into infestation of 67 percent of the entire bark surface. It is nearly 3 times as abundant as any other species." He also found that unmixed infestations of the western pine beetle were common in eastside areas, but uncommon in westside areas. In both areas, the beetle commonly extended the attack to about a 4-inch top diameter.

Figures 25 and 26 compare the infestation types on westside and eastside pine areas in 1934. Control records were used to map infested bark areas by insect species for all trees containing 1933–34 overwintering broods on Regional Survey Plot 7 (Cascadel area)

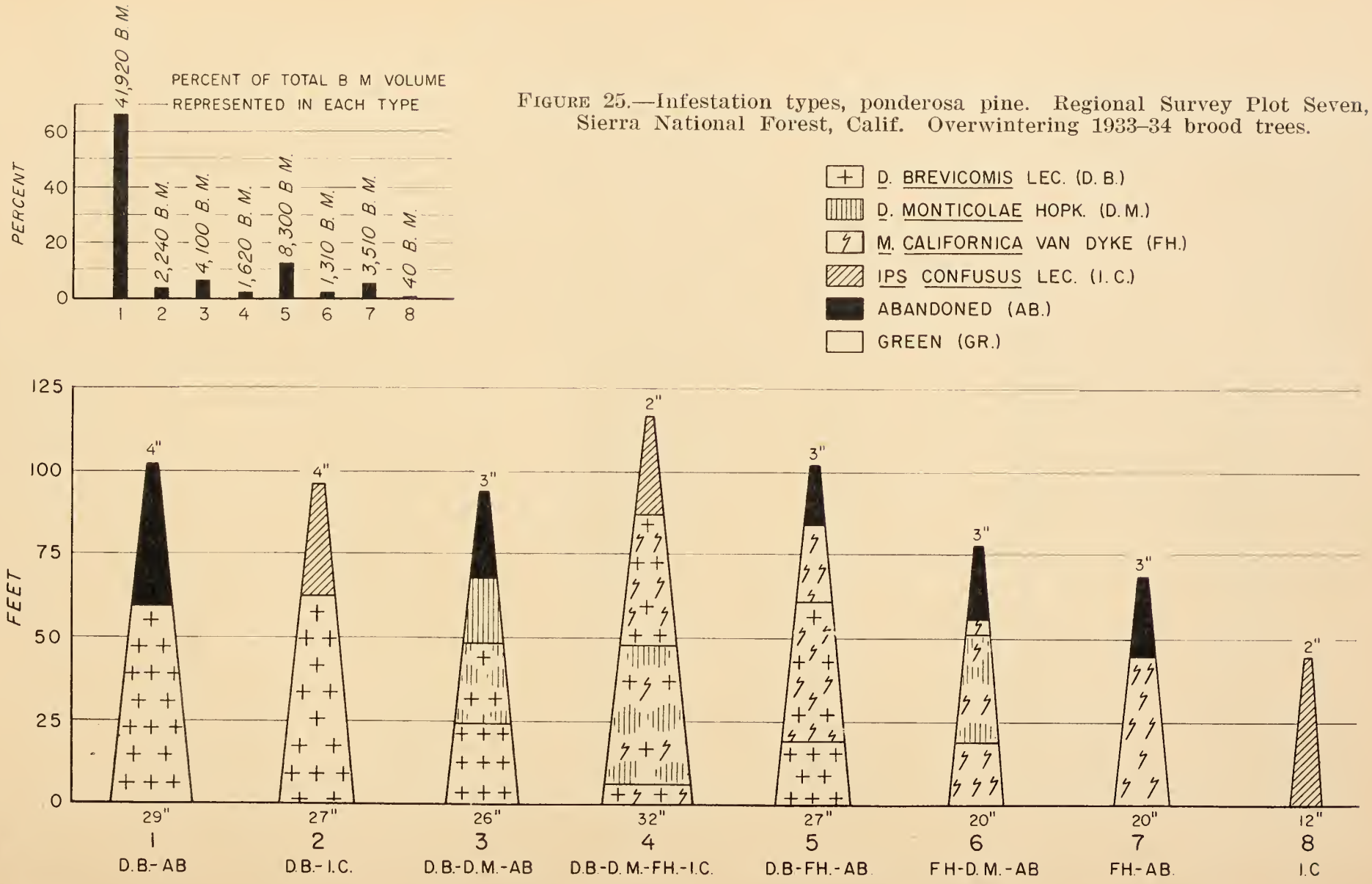

FIGURE 25.—Infestation types, ponderosa pine. Regional Survey Plot Seven, Sierra National Forest, Calif. Overwintering 1933–34 brood trees.

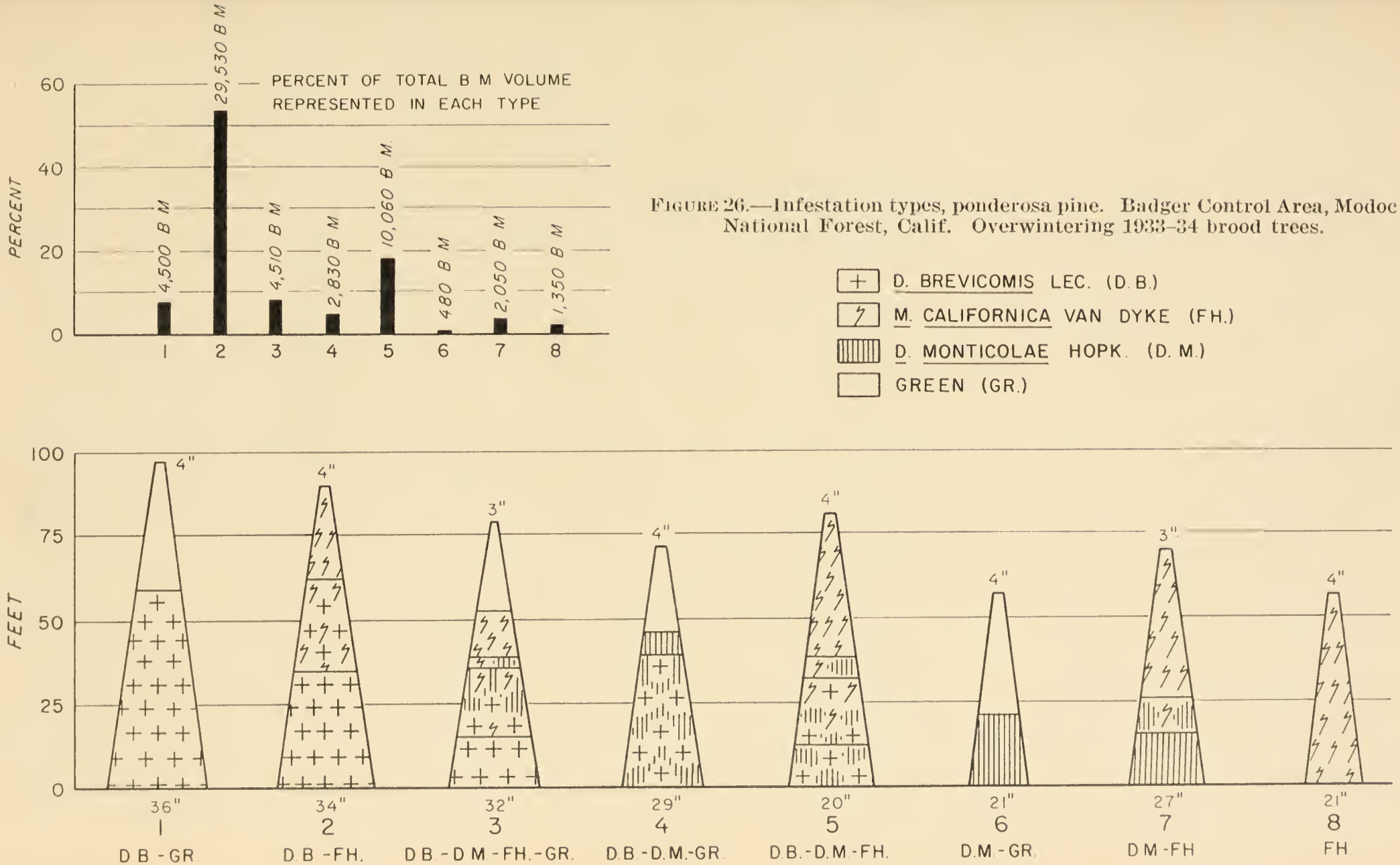

FIGURE 26.—Infestation types, ponderosa pine. Badger Control Area, Modoc National Forest, Calif. Overwintering 1933–34 brood trees.

representing the westside pine type, and the Badger Control Area (Modoc) representing the eastside type. In these figures, average diameter and height of trees making up each infestation type are drawn to scale, so that the relative size of trees involved in the different composition is shown. The percent of total infested volume that each infestation type composed is also illustrated.

The westside infestation types were made up primarily of trees that had been initially top-killed. At the time of the western pine beetle attack, they were either infested or abandoned in the top by engravers and flatheaded borers. In the eastside types, top-killing was a minor factor—four of the eight types had no insect attack at all in the top. The eastside types were primarily a western pine beetle–flatheaded borer composition, with the mountain pine beetle playing a more prominent role in the midbole than on the westside areas.

Salman (*U271*) recognized 22 combinations or types of mixed infestations but listed 3 as the most important for the region as a whole:

1. *Western pine beetle–flatheaded borers.*—This type of infestation was found to be the most important in eastside areas and fourth in importance in the westside areas. The combination of the 2 species may extend from the base to the top of a tree, or may exist with pure flatheaded borer infestation in the top, or pure western pine beetle infestation in the bottom. It also may exist only in the middle bole with pure flatheaded borers in the top and pure western pine beetle in the bottom.
2. *Western pine beetle–engraver beetles.*—This combination was the more important in westside areas due to the outbreak of engraver beetles (*Ips confusus*) that occurred in those areas during the period of record. It is believed that the western pine beetle is secondary in these trees as many of them were of small size and the engraver beetle initiated the attack. In the eastside areas *Ips oregoni* is the species concerned. Evidence was found that the engraver beetles here followed the initial attack of the western pine beetle.
3. *Western pine beetle–mountain pine beetle–flatheaded borers.*—This mixture of species in which either the first or last named may be primary and the mountain pine beetle usually of secondary importance appears to be predominantly an eastside infestation type.

Salman (*U271*) pointed out that "marked differences in infestation composition are noted between the eastside areas, which lie in the 0- to 20-inch precipitation belts, and the westside areas that lie in the 20- to 40-inch precipitation belts." Eastside types differ from westside ones by "(1) the greater amount and importance of mixed infestations, (2) an increased importance of flatheaded borers, (3) decreased importance of engraver beetles, exclusive of *Ips emarginatus*, and (4) the western pine beetle entering into a greater proportion of the infested bark." He attributed these differences largely to variations in moisture supply.

The reliability of basal examinations as an index to primary insects attacking the main bole was another phase of this study. Salman (*U271*) found that "basal examinations would determine

the cause of death in the predominant infestation types in but 36 out of every 100 trees. Cruise results interpreted strictly on the evidence from basal examinations may show the relative abundance of a given species but not necessarily its importance." Salman recognized that "the western pine beetle is the most abundant insect concerned in forest insect infestations of ponderosa pine in California," but thought that "its primary importance may be overrated. . . . The data show that so-called secondary species, particularly *Ips confusus* and *Melanophila californica* may, in infestations over relatively large areas be the primary species and cause the death of the majority of infested trees."

These studies were not continued long enough to show the significance of variations in composition from year to year, or to obtain clues as to what such variations might mean as indicators of changes in the infestation cycle.

Studies of Infestation Types in Northeastern California, 1937–41

From these preliminary studies, investigators thought that annual changes in the composition of attacks upon ponderosa pine might be significant in infestation cycles. Therefore composition studies were continued after 1935 in northeastern California. These studies were given considerable impetus by a growing realization of the importance of the California flatheaded borer in the ecology of eastside pine stands.

Data were collected each year from a sample area on which the infested trees were felled, and areas of infested bark were measured. As stated by Johnson (*U115*),

> The studies of species relations in the infestations of ponderosa and Jeffrey pines were begun because of a need for more knowledge of such phenomena than had been obtained from the usual field examinations of standing trees. Attention was directed to 4 specific objectives.
>
> 1. To determine what insect species had attacked the trees.
> 2. To determine the sequence of the attacks of different species on trees and their interrelationships in the infestations.
> 3. To determine the relative frequency of the different species, and the fluctuations in their numbers from year to year.
> 4. To discover the infestation patterns characteristic of the different years.

In 1938 West (*U326*) reported upon composition studies made in 1937 and 1938 on Modoc National Forest. He noted a difference in the grouped tendency of attacks between these two years. In 1937, 12 percent of the attacked trees occurred in groups; in 1938, 44 percent. The principal species in these infestations were western pine, mountain pine, and red turpentine beetles, the Oregon pine engraver, and the California flatheaded borer. Of the trees selected for attack in 1937, 37 percent had been previously top-killed, as against 42 percent in 1938. The Oregon pine engraver was important as a fill-in species in trees initially attacked by the western pine beetle. The California flatheaded borer was found in 61 percent of the trees attacked in 1937, but in 1938 in only 41 percent.

In 1940 Johnson (*U111*) compared the trends and composition of infestations that developed during the 1939 and 1940 seasons on the same sample area. These two seasons were characterized by fairly low infestations and by a marked decline in number of trees killed between 1939 and 1940. This decline was accompanied by recognizable changes in the composition of the attack, as can be seen from the following tabulation in which the species initiating the attack is listed first:

Infestation type:	Percent of total trees	
	1939	1940
Melanophila californica–Dendroctonus brevicomis	14.1	39.5
M. californica–D. brevicomis–Ips oregoni	14.2	25.6
M. californica–D. monticolae–D. brevicomis– miscellaneous	8.4	2.3
D. brevicomis only	18.3	9.3
D. brevicomis–I. oregoni	45.1	14.0
I. oregoni–D. brevicomis	2.8	7.0
D. monticolae–D. brevicomis	5.6	—

Johnson (*U111*) compared the seasonal composition in trees attacked in groups and singly, and found that:

D. brevicomis had a higher incidence in group trees than in single trees, and its incidence in both classes of trees decreased from 1939 to 1940. *Melanophila californica* had a higher incidence in single trees than in group trees, and its incidence shows an increase from 1939 to 1940. *Ips oregoni* shows its highest incidence in group trees and shows a slight increase from 1939 to 1940. But it is noteworthy that the *Ips oregoni's* general occurrence in all infestations, both as initiating species and as a supplemental species, was less (46.5 percent) in 1940 than in 1939 (53.5 percent). *D. monticolae* disappears from the picture in 1940. In 1939 its incidence was slightly higher in single trees than in group trees.

In 1941 Johnson (*U115*) studied the 1940 and 1941 infestation types in both ponderosa and Jeffrey pines on Lassen National Forest. Points brought out in his summary for this area included the following:

Dendroctonus brevicomis was the most frequent species in the infestations in both years.

Melanophila californica was the second most frequent species in both years.

Dendroctonus monticolae, *Ips emarginatus*, *Dendroctonus valens* and *Ips oregoni* were of common occurrence in the infestations, the first three species being relatively more numerous in 1941 than in 1940.

Summary of Composition Studies

Johnson's (*U115*) studies were the last of the composition surveys, and in attempting to appraise the value of the work he stated: "From the composition studies has come a better appreciation of the complexity of the inter-insect and inter-tree relationships that develop during the death of the tree from insect attack."

The studies did not carry the understanding of species relationships in mixed infestations far enough to warrant its use in appraising the status of current infestations and in forecasting trends. Nevertheless, these conclusions appear to be warranted by the data:

1. Practically all of the western pine beetle infestations studied were of a mixed type. Associated insects played a prominent role.
2. Basal examinations seldom provided a reliable index to the type of infestations in the main bole of the tree (in only 36 of every 100 trees). In bark beetle surveys, the judgment of the spotter must largely determine the type of infestation in trees that are marked as infested.
3. Where infested lengths have been studied, composition of the infestation varied greatly from season to season and between areas.
4. There is good evidence that the relation of species composing a current infestation may serve as an index to coming trends. When the season is marked by aggressive top-killing by engravers or flatheaded borers, an increase of western pine beetle will follow (as on the Sierra area). When the western pine beetle occupies nearly all of the infested bark surface and engravers and flatheaded borers are a minor factor, a decline of losses may follow (as on the Modoc).
5. Western pine beetle is the dominating species in the composition when the peak of an epidemic is reached.
6. The work of obtaining accurate bark-surface measurements to show the quantitative composition of a mixed infestation is time consuming and impractical in survey practice. This factor has obviously discouraged the use of composition analyses as a basis for determining the expected trend of infestations.

EPIDEMIOLOGY OF THE WESTERN PINE BEETLE

The Interaction of Biotic Factors

For many years it was assumed that the population of beetles produced at any one time must have some direct relation to the number of trees attacked and killed by these beetles after emergence and flight. In fact, direct control procedure was predicated upon the hope that killing a large number of developing broods would greatly reduce the losses of timber from their progeny. It was not until 1928 that Keen (*U142*), analyzing 15 years of brood counting, cast doubt upon this premise. He concluded that "there is no relation between emergence per square foot and subsequent infestation." Further,

> This study indicates that the small fluctuations in attack, brood development, and emergence with individual trees during different years have little or no significance in accounting for the rise and fall of epidemics. Instead, the important factors appear to be operative during the flight period—after the beetles leave the trees and before they make a successful attack upon their new hosts.

After studying the trend of western pine beetle infestations on Modoc National Forest in California during 1933, 1934, and 1935, Salman and Bongberg (*U283*) concluded:

> It appears that, even though there be a large number of infested trees in an area, it is not necessarily true that there is a great hazard of further heavy losses. It also follows that a few infested trees, in terms of their relative potential hazard, may be much more important than a larger number of infested trees. Apparently the amount of loss or the density of population has no constant relation to the hazard to the timber from subsequent attacks by descendents of that population.

The amount of timber killed in any given area each year is determined by the interplay of many factors of which beetle population is only one. Salman and Bongberg (*U283*) state:

> The fluctuations in timber loss supposedly caused by the western pine beetle go to make up what are known as infestation cycles. The increases, as they have occurred, have largely been considered due to the potential power of the insect species or to the susceptibility of the host trees. The decreases in the loss record have largely been considered due to the reduction in populations of the western pine beetle, a resistance of the host trees, or adverse climatic factors. At times sudden changes are inexplainable. Three years of study of the biology of the western pine beetle has indicated that the story of the fluctuations that occur in the records of insect-killed ponderosa pine is not a simple one.

Periodicity Studies

Even though the causes cannot be determined, a knowledge of the frequency with which epidemics or high peaks of population occur is of advantage in dealing with the western pine beetle. Knowing when to expect outbreaks, the owner of threatened timber could prepare for control work or for utilization of stumpage before it is killed. Therefore the possibility of forecasting changes has been one incentive for the maintenance of long-term survey records showing the rise and fall of beetle populations that have been measured by the amount of timber killed annually.

Rogue River Studies, 1914–24

The first study of western pine beetle epidemiology was started at Ashland, Oreg., in 1914. In preliminary studies, Keen (*U133*) analyzed the infestation on the Lamb's Mine Unit of 3,200 acres for the seasons of 1914, 1915, and 1916. Types of infestation and changes in quantity of losses were itemized from season to season. Losses were rising during most of this period, and Keen pointed out that "this quantitative study will become more valuable when the quantity for the next few years is measured each year."

The Lamb's Mine area, however, was suspected of being too small a unit for an adequate sample of broad infestation trends in the pine type. The study was therefore expanded in 1916 to include about 350,000 acres, more than half of which was ponderosa pine type, in the Rogue, Applegate, and Klamath River watersheds. This area contained a wide variety of climatic and site conditions and was considered large enough to represent any significant changes in trends that might occur during the study.

The first report for this enlarged study area was prepared by Miller (*U178*), who stated that one purpose of the study was to determine "the character, periods of time involved in, and the causes of the intermittent increase and decrease in the annual amount of infestation."

The Rogue River and Klamath areas were divided into a series of 19 watershed units; timber losses were measured separately in each unit. The Applegate area, in which the pine type was scattered and broken, was treated as a whole. The loss records

on all of the areas began with the 1914 season, but on two of the Klamath units old loss cruises carried the record back to 1911. Survey intensity varied in the different areas. Most of the Rogue River units were cruised intensively; the Applegate watershed was covered by extensive reconnaissance; in the Klamath area two units were covered by intensive loss surveys, and the remainder were covered by extensive methods. In all areas the intensity was considered accurate enough to reflect loss trends.

Miller summarized the first 4-year results (1914–17) as follows (*U183*):

> *Dendroctonus brevicomis* is by far the most important enemy of the pine and is responsible for 90 percent of the total annual loss. The loss caused by this insect does not remain constant, but is subject to great fluctuations from year to year. In this study the *D. brevicomis* infestation underwent a distinct cycle or epidemic covering a period of 4 years, during which a pronounced increase was followed by a corresponding decrease.
>
> The epidemic which has been studied ran through approximately the same cycle throughout the entire project area of 350,000 acres. The cycle of the infestation within each of the small tributary watersheds which have been termed units was nearly uniform throughout the project area. The high-water mark of the epidemic occurred in 1915 on some units and in 1916 on others. But we do not find a single case of any unit declining to a low point in 1915 or 1916, but in all units studied the epidemic started upward in 1914 and declined in 1917. This indicates that the factors which influence the rise and decline of epidemics are not confined to small local centers or watersheds, but operate throughout great forest areas.

These conclusions indicated rather definitely that it was unnecessary to cover so large an area to obtain a record of trends within a region. The recommendation was made, therefore, that the Applegate and Klamath areas be dropped from the surveys, but that the study on the Rogue River area be continued "until such time as sufficient data on all phases of the infestations were secured to make possible the forecasting of epidemics and their probable duration." Patterson continued the work until the close of the 1924 season. His 1924 report (*U221*) summarized the infestation cycles in the Rogue River area during the 11-year period 1914–24:

> The first epidemic infestation occurred in the years 1915 and 1916, killing during this period 1.9 percent of the stand. This was followed by a decline of 56 percent during 1917. In 1918 the infestation again became epidemic, killing .7 percent of the stand: an increase over 1917 of 78 percent. From 1918 the infestation gradually declined with minor fluctuations until 1923, when it reached the lowest point recorded, killing only .13 percent of the stand. From this point the infestation showed a decided upward trend and in 1924 made an increase over 1923 of 82 percent. The infestation may continue to mount in 1925 or it may decline as it did following the 78 percent increase in 1918.
>
> One striking feature of the progress of the infestation is the regularity of the 4-year cycles. Beginning with the low point in 1914, the subsequent low points in 1917 and 1921 showed 3-year

intervals. Likewise the peaks occurred every fourth year beginning with 1915 and followed by the peaks in 1918 and 1922. If the study of other infestations show similar results, we may expect relatively high infestations with heavy losses every fourth or fifth year.

The percent of stand killed annually on the entire area and the loss cycles mentioned by Patterson during the period 1914–24 are shown in figure 27.

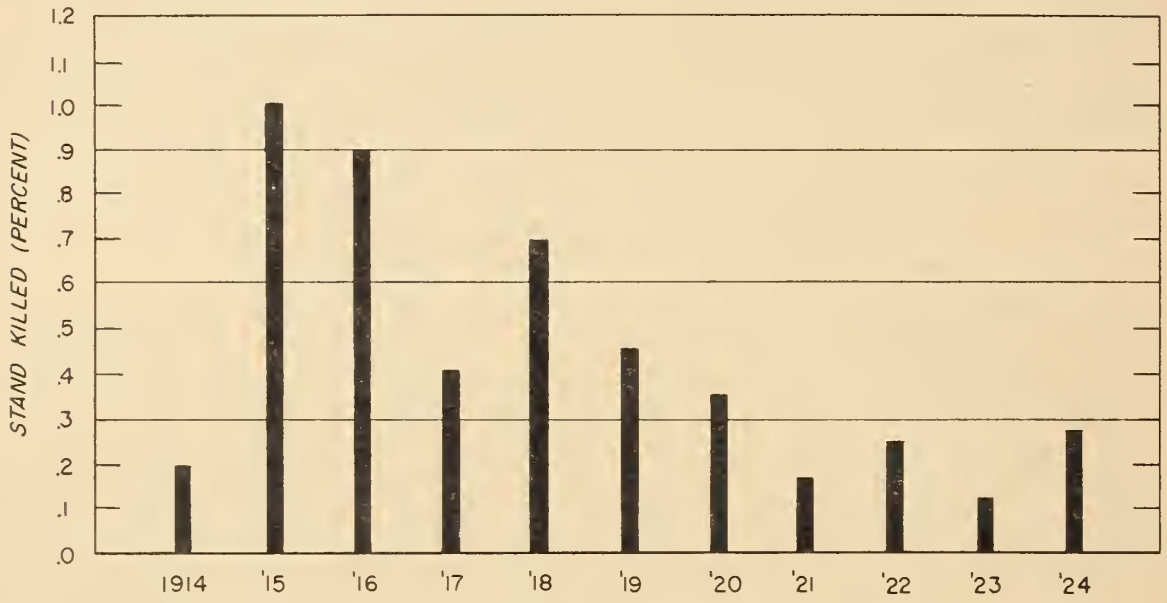

FIGURE 27.—Western pine beetle infestation trend on Rogue River area, Oreg., 1914–24.

The Rogue River study was discontinued in 1925. The pressure of control surveys in other areas was one reason. Furthermore the mature pine type in many Rogue River watersheds had deteriorated, as a result of wood cutting, timber operations, and beetle losses, until it was no longer suitable for a study of undisturbed infestation trends.

The Klamath Basin Records, 1921–52

Surveys were inaugurated in the Klamath Basin as early as 1911, but the first 10 years' data did not provide the quantitative basis for an accurate interpretation of infestation trends. In connection with the Southern Oregon–Northern California Pine Beetle Control Project, however, check plots were established in 1921. They were scattered over the main ponderosa pine forests of Klamath and Lake Counties, Oreg. While the control project was underway, 120 plots of 640 acres each were cruised to determine the general trend of the infestation and the need for control in different units. The territory included about 1,250,000 acres divided into three roughly equal areas. On some plots the loss record was extended back to 1918 on the basis of control surveys.

After the cooperative control funds were exhausted and each agency continued control work independently, such a large cruising program could not be continued and some plots were dropped. Year by year, with the advance of logging operations, other plots had

to be dropped. By 1933 only 25¼ sections remained to continue the record of annual losses. Plot records and estimates of total annual kill from 1921 to the close of the 1932 season were reported by Keen (*U139*, *U149*). Subsequent annual surveys have continued the loss record in this region.

Several trends were evident in the loss record from 1921 to 1931 (*U149*):

> As has been pointed out several times before, the trend of bark beetle infestation has not been uniform over the entire area represented by the sample plots, even though the growth pattern has been practically identical for the entire area.
>
> Thus *area 1* plots reached a high point in 1925, decreased to a low in 1928, increased slightly in 1929, dropped again in 1930, and started up again in 1931.
>
> *Area 2* plots reached a high point in 1926, decreased steadily to a low in 1930, and then started up in 1931.
>
> *Area 3* plots reached a high in 1927, dropped suddenly to a low in 1929, and then started up in 1930.
>
> Evidently there is a complicity of factors which determines epidemic trends; and while tree resistance is an important one, the character of the stand, the amount of recent bark beetle losses, and the action of predators all have their influence in determining the course of a beetle epidemic.
>
> Moreover, climatic factors are of prime importance as is so well illustrated by the effect of the recent low winter temperatures which destroyed a high percent of the bark beetle broods throughout the pine region of eastern Oregon.

After 1931 the infestation in the Klamath Basin reached a new high in 1932; it then dropped in 1933 owing to severe cold weather in the winter of 1932–33, recovered somewhat in 1934, and then dropped to a new low in 1937. After 1937 the infestation increased to a minor high in 1939 and then dropped to an all time low in 1942. This was the lowest point reached after records were started in 1921. After 1942 the infestation continued at an endemic level for 10 years, never exceeding an annual loss of more than 0.60 percent of the stand per year (fig. 28).

About 1930, it was thought that the infestation trends in the Klamath Basin with lows in 1917, 1923, and 1929, supported the theory of a 6-year cycle. But then lows occurred in 1933, 1937, and 1942, and after 1942 a state of low endemic infestation continued for 10 years. Thus the theory of epidemic cycles breaks down; explanations of the rise and fall of epidemics must be found elsewhere.

Northeastern California Records, 1921–43

Other longtime records of losses caused by the western pine beetle and associated insects are available from northeastern California—on the Happy Camp-Lava Beds area of the Modoc and Shasta National Forests beginning in 1921, and on the eastern Lassen and Plumas National Forests beginning in 1929. Although many of the original plots were lost through logging operations, annual surveys provided continuous estimates of the board-foot loss per acre in virgin stands.

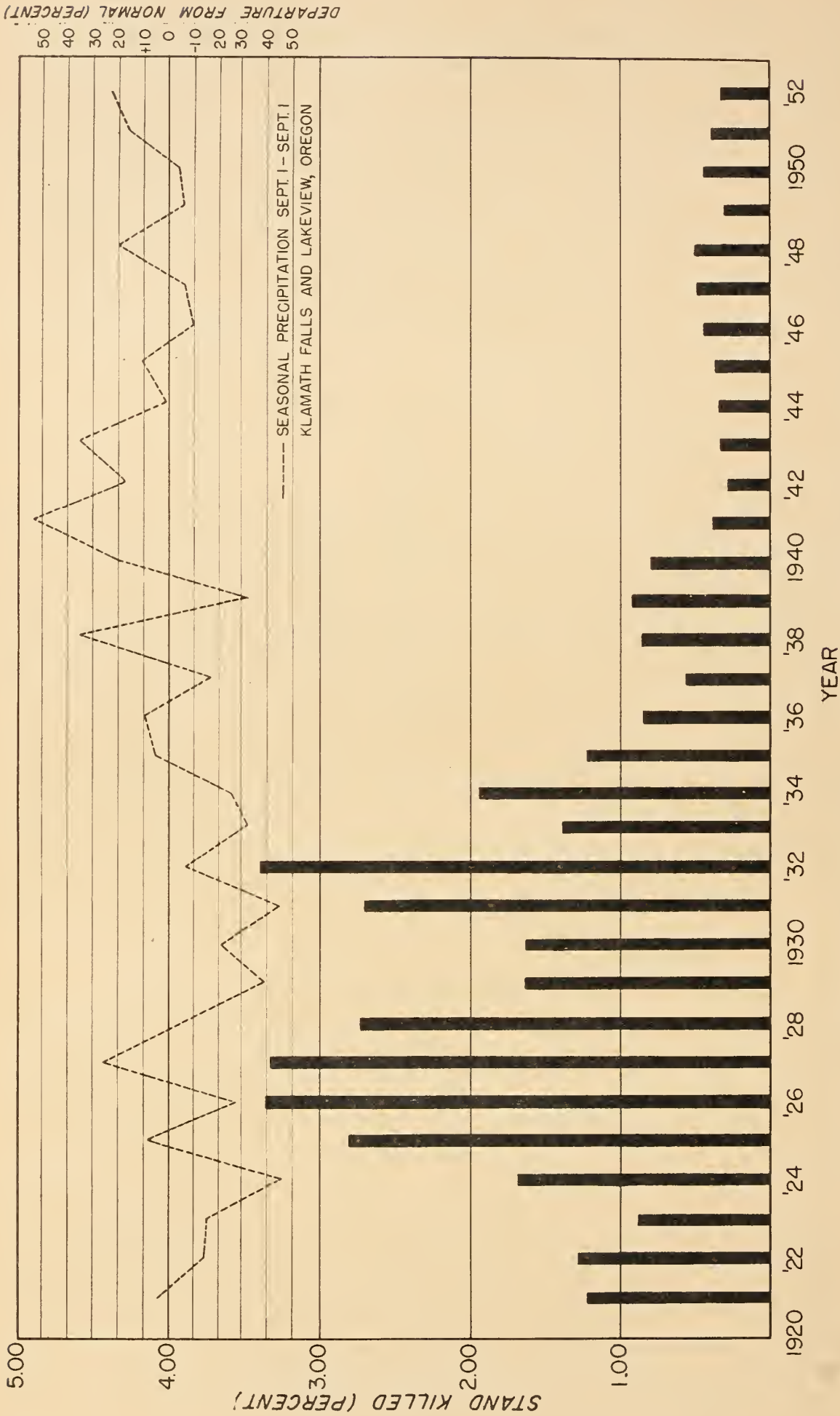

FIGURE 28.—Trend of western pine beetle infestation in the Klamath Basin, Oreg., 1921–52

On the Happy Camp-Lava Beds area, peak losses in the period 1921–49 occurred in 1927 and 1934 (fig. 29). The trend is strikingly similar to that in the neighboring Klamath Basin (fig. 28). Some variation is evident, however, in the four individual units of the Happy Camp-Lava Beds area for the period 1921–35 (fig. 30).

These records were partially analyzed by Hall (*U80*), who made a study of the trends for the Modoc area, 1923–38, and the Lassen area, 1930–38. The records for the Lassen area were available only for the second seven-year cycle, but the trend corresponded very closely with that on the Modoc. After presenting the losses in graph form, Hall stated: "This figure tends to show that there appears to have been 2 distinct cycles in losses since 1923. These appear by 7 years duration with the peak in both cases having been reached the fourth year following the low point in the cycle."

Although the period 1921 to 1937 showed some evidence of two 7-year cycles, the period after 1937 gives little basis for support of the cycle theory. Like the Klamath Basin, this area since 1941 has been characterized by an extremely low level of endemic infestation. One reason for this low level may be the contraction of virgin stands owing to extensive selective cutting. Cutting has narrowed the field of beetle activity and reduced the chance of epidemics by depriving the beetles of susceptible breeding material. Another probable reason is the successive years of above-average precipitation since 1940; better moisture improves tree growth, increases tree resistance, and lowers losses.

The Westside Sierra Studies, 1912–43

The longest record of beetle-caused losses is from Sierra National Forest in the westside pine type near North Fork, Calif. Control work started here in 1912, and loss measurements on selected sample

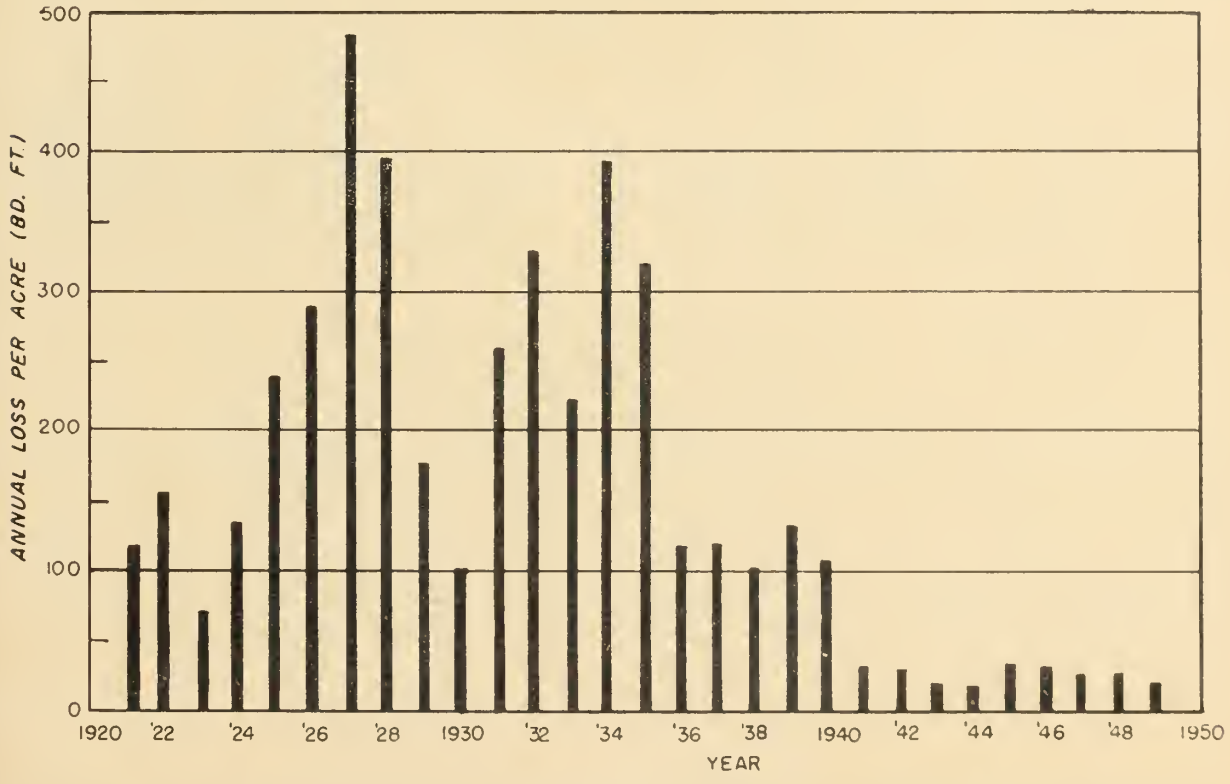

FIGURE 29.—Trend of western pine beetle infestation on virgin ponderosa pine sample plots, Happy Camp-Lava Beds area, Modoc National Forest, Calif., 1921–49.

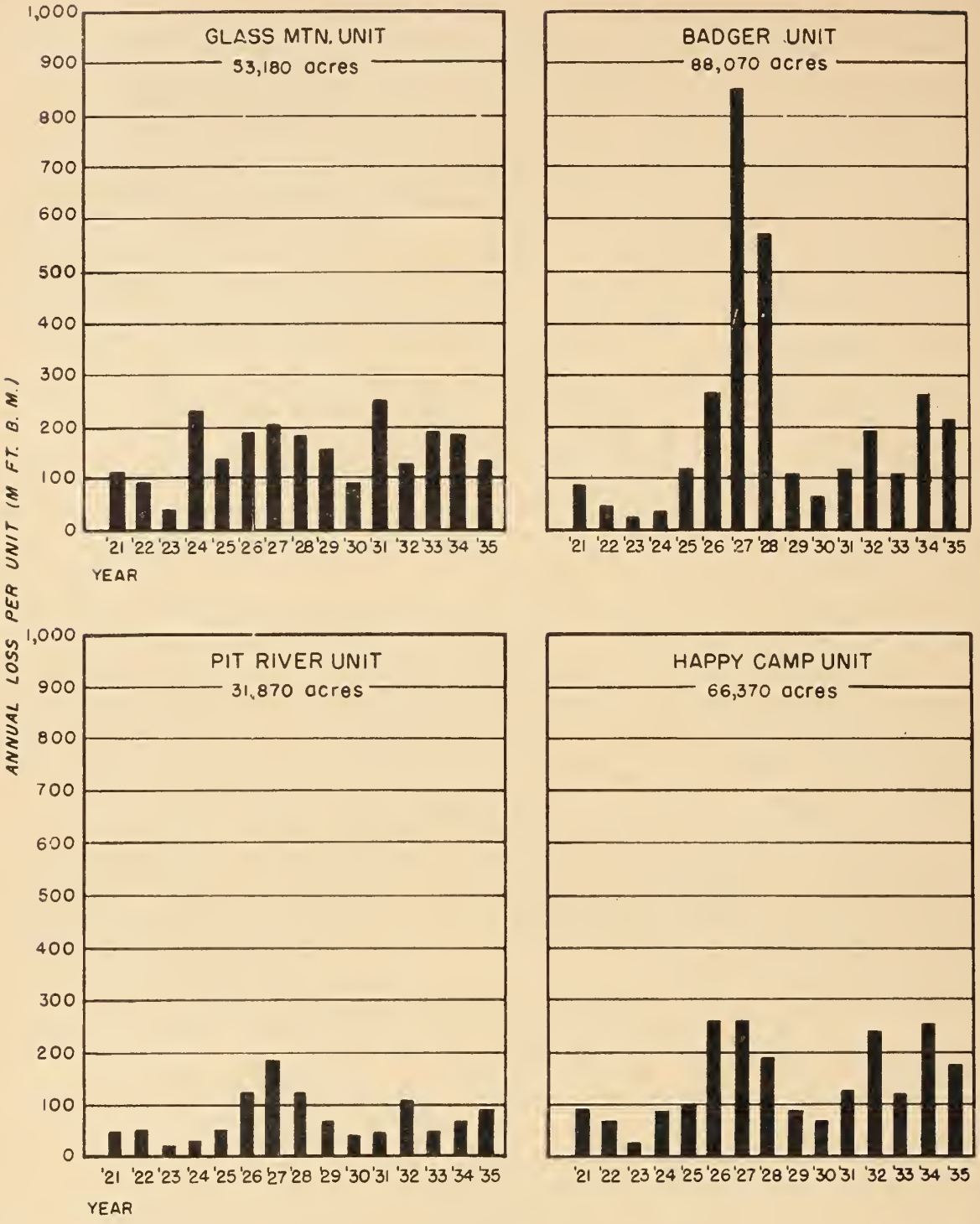

FIGURE 30.—Estimated volume of ponderosa pine killed annually on four units, Happy Camp-Lava Beds area, Modoc National Forest, Calif., 1921–35.

plots were started in 1929. Thus although accurate measurements are not complete, the record includes data from control work by the Forest Service and from special studies by forest entomologists during nearly all of the time until 1943. Enough data are available to reflect the high and low points in the infestation for 32 consecutive seasons. In discussing these trends, Miller, Struble, and Hall (*U209*) stated:

One characteristic of the beetle-caused loss record of the pine type of the Sierra is the irregularity of the annual kill, although there is some indication of a cyclic tendency during certain periods. If we look at the graph representation of the losses from 1912 to 1942, we find long periods of low loss levels below 200 board feet per acre interrupted by very brief periods when the loss rose above this level. Most striking of all are the years 1930–1932 when the loss rose sharply to a point in excess of 10 times the average for the preceding 19 years.

The graph referred to (fig. 31) shows annual board-foot loss per acre, together with seasonal precipitation.

Much of the report just quoted is given over to the causes of the fluctuations in losses. This is a very complicated field dealing with the ecological relations of the western pine beetle and requires an analysis of the factors affecting the host tree.

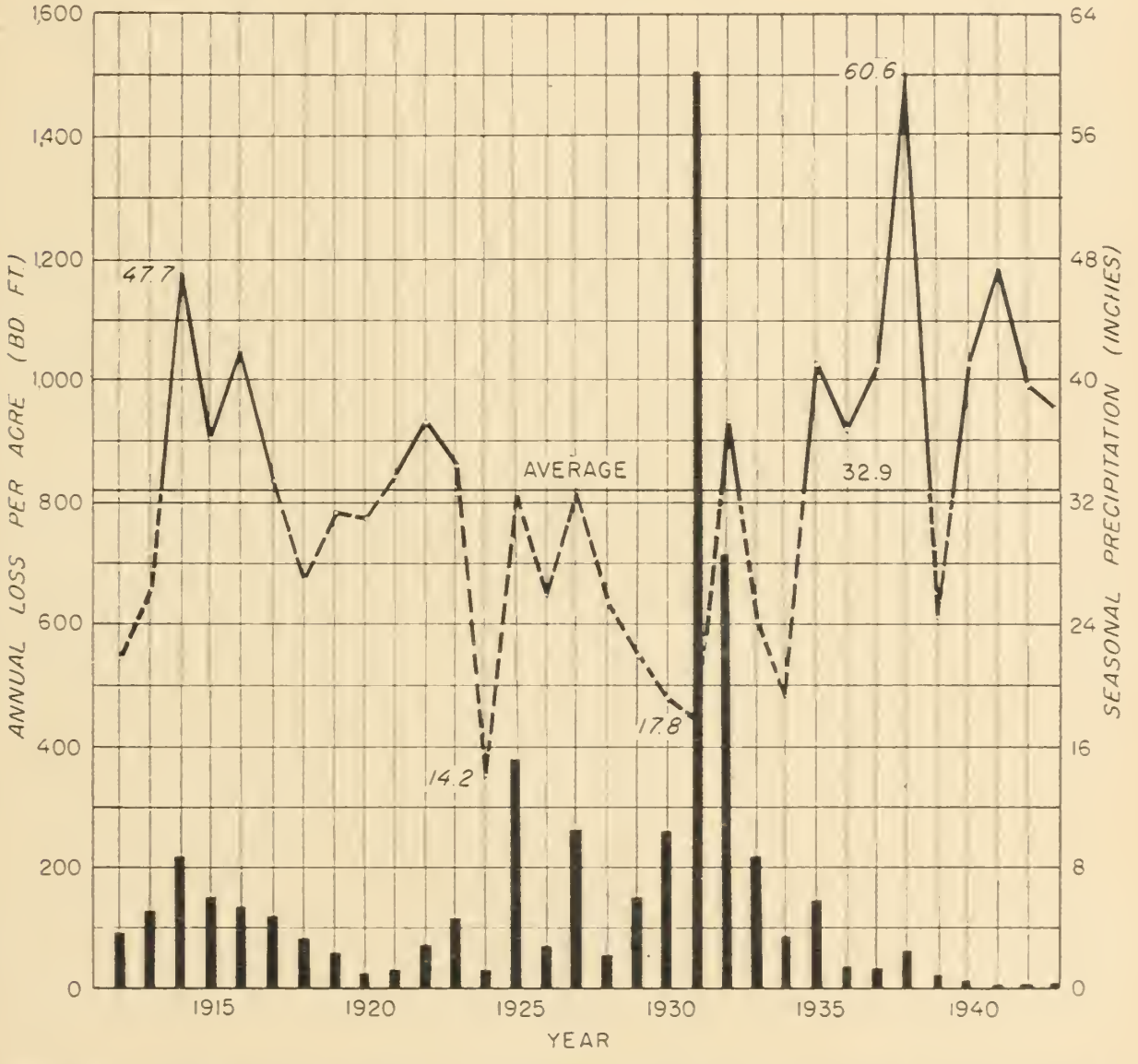

FIGURE 31.—Relation between precipitation and pine mortality due to bark beetles, 1912–43, Cascadel area, Sierra National Forest, Calif.

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SECTION III. RELATIONS BETWEEN BEETLES AND HOST TREES

Another important set of factors affecting the success or failure of western pine beetle attacks may be found in the insect-host relationships. Some trees offer strong resistance to attack, others are easily overcome. These two contrasting conditions, resistance and susceptibility, are associated with the physiological influences that produce vigorous tree growth—heredity, age, crown size, position, site, soil fertility, moisture, climate, and silvicultural conditions in the stands. All of these factors influence the epidemiology of the beetle by operating indirectly through the host plant (*20*). This section reviews studies of the tree's reaction to beetle attack and of the ecological and environmental factors that determine the tree's ability to resist.

THE EFFECT OF ATTACK UPON THE HOST TREE

The attack of the beetle upon its host tree represents a two-way biological relationship. Both begin as living organisms, and each reacts to certain stimuli produced by the other. The beetle may select some particular tree, either by chance or attraction; the tree, through healing and growth processes, attempts to resist the attack until the beetle is pitched out by resin flow or the tree succumbs.

Immediate Reactions of Living Trees to Attack

Mechanical Injury and Resin Flow

An attacking beetle boring through the corky layer of outer bark causes no damage to living tissues of the tree. However, as soon as it reaches the phloem layer, the beetle encounters living cells. These are made up of (1) the conductive tissues that transport soluble starches and sugars, (2) the storage cells that hold these materials until they are built into wood, and (3) resin canals that conduct and store the oleoresin ("pitch") that serves to seal wounds. The beetle may barely score the sapwood as it advances its tunnel through the phloem, but it bores no deeper into the tree.

The effect of these first phases of the attack on the tree is apparently identical to reactions produced by mechanical injury—much the same as if a hole were drilled through the same layers of plant tissues by a tiny auger. As the resin canals are severed, pressure is released and a flow of pitch exudes into the wound. This flow is the first response of the tree to attack and apparently constitutes its first and only line of defense against invasion by the beetle.

"Pitching Out"—An Indication of Tree Resistance

The pitch flow apparently causes the beetle no end of irritation. If allowed to dry in the entrance hole, the gummy pitch gradually hardens and plugs up the opening. To prevent this, the beetle

manipulates the pitch out to the surface of the bark and builds a pitch tube. Successful attack is not accomplished until the exudation of pitch ceases. A continuing abundant flow of pitch over a long period results in either death of the beetle or abandonment of the attack. This result, known as "pitching out," may be due to exhaustion of the beetle or to the toxic effects of the turpentine or resin acids that make up the pitch.

A few attacks on a vigorous tree will always pitch out, but concerted attacks over a large percent of bark surface usually result in drying the sapwood and impairing the tree's ability to produce resin. When this occurs, attacks are successful. In many cases attacks fail either because of the strong flow of pitch or because the beetles did not attack in sufficient numbers to overcome pitch flow.

Considerable effort has been directed toward finding the basic factors that enable certain trees to resist attack successfully. If resistance can be attributed to resin flow, then the differences between individual ponderosa pine trees may be related to variations in the quantity or quality of resins produced. Or they may be related to other resin characteristics such as resin pressure or rate of flow. Mirov (*U210*) made a preliminary study of resin production in 1928 and reported: "Some turpentining experiments by the U.S. Forest Service in California showed that the chemical composition of oleoresin from different specimens varied greatly."

The amount of resin produced also varies greatly between individual trees. This has been generally accepted as related to growth vigor. However, Mirov (*U210*) reported:

> Usually considerable stress is laid upon the pitch yield of trees on the supposition that slow growing trees if attacked by bark beetles produce a smaller amount of oleoresin than fast growing trees, and thus are less resistant to attack. . . . During the turpentining experiments, it was found that there is very slight, if any, correlation between growth rate of oleoresin exudation.

To determine tree resistance to bark beetles, Callaham and Miller (*U51*) conducted some studies with various pine hybrids in 1951 at the Institute of Forest Genetics, Placerville, Calif. Besides showing that oleoresins of Jeffrey pine and Jeffrey-ponderosa pine hybrids appeared to be toxic to the western pine beetle, the tests also indicated that "when an insect can tolerate the oleoresin of a given pine, then the quantity of resin produced by individual trees becomes a critical factor in the success or failure of an attack."

Further tests of pine resistance to bark beetles were made by Callaham in 1952 (*U50*). Since digger pine, Torrey pine, and a hybrid of knobcone and Monterey pine were found to be resistant to the western pine beetle, Callaham postulated that any pine having more than 20 percent n-heptane in its turpentine would be toxic to this beetle.

After 1952, Callaham continued a series of comprehensive studies to determine the relation of oleoresin quantity, flow, and pressure, and the effect of various constituents of oleoresins upon tree resistance and the success of western pine beetle attacks.

Effect Upon Transpiration and Growth Functions

As a successful attack becomes established, the egg galleries are extended through the phloem in a crisscross pattern until the tree has been completely girdled. This phase of the attack effectively breaks down the tree's circulatory system. Water and food materials in solution can no longer be transported up and down the main trunk. The effect upon the wood-building functions is therefore immediate, and cambial growth soon ceases. However, since the foliage is still intact and can obtain water for transpiration from the stored water in the stem, the needles remain green for some time after the attack is established. When the stored water is exhausted, the needles dry and lose their green color. On the whole, the egg galleries produce an effect similar to that observed in a pine that has been girdled to sapwood depth with an ax.

Beetle-attacked trees die much more quickly than mechanically girdled ones (which may remain green for a year or two) because the girdling process of the beetle involves considerably more than the mechanical injury to the tissues. When the beetles open up tunnels into the phloem area, air enters and dries out the sapwood cells beneath these tunnels. Next, a blue-stain fungus is introduced, either by the beetle or by wind-blown spores that find entrance into the egg galleries. This fungus attacks the sapwood. It does not destroy the wood cells, but blocks their capacity to conduct water to the foliage. As a result of the combined work of the beetle and the blue-stain fungus, the needles are deprived of water, transpiration ceases, and the needles lose their chlorophyll and turn straw color. Then the tree, for all practical purposes, can be classed as dead.

Time Required for Beetles to Kill a Tree

The time it takes a tree to go through the process of dying varies with the season, with the resistance of the tree, and with the amount of time required by the beetles to establish a complete attack. As Keen (*U130*) pointed out, "the attack may extend over a long period of time, advancing gradually from the top of the tree downward; or the attack may be made more or less simultaneously on the entire length of the main bole and become established within a week or so." In the latter case, the tree dies rather rapidly if temperatures are warm enough to produce rapid evaporation of moisture in the foliage and to stimulate development of the blue-stain fungus.

Person conducted intensive studies of attack on a series of caged trees near North Fork, Calif., during the seasons of 1926 (*U238*) and 1927. After the 1927 work he reported (*U241*):

> The difference in the period between attack and the death of the tree, for trees killed during the first flight period and during the second flight period, is very marked; an average of 42 days for the first and only 8 days for the second. Most of the difference is undoubtedly due to the much colder weather in the spring which makes the beetles less active . . . Another cause for this difference may be that the trees are much less resistant during July

and August when the available moisture is low and the physiological processes are slower.

Death of Tree Recorded by Dendrograph

To measure the effect of attack upon tree growth, Person (*U241*) used two dendrographs of the type developed by Dr. D. T. McDougal of the Carnegie Laboratory at Carmel, Calif. These instruments record with considerable amplification and accuracy the changes in diameter of a tree at a point just outside the phloem area. During the seasons of 1926 and 1927, one dendrograph was used to record the daily and seasonal growth of a tree of normal growth behavior; the other was used to record the behavior of a tree that died as a result of forced attack by the beetles.

The check tree showed a daily fluctuation in diameter—a shrinkage during warm hours of the day when transpiration from the foliage was rapid, and a swelling during night hours and during cold periods of the day when transpiration slowed down. These diurnal changes in diameter apparently reflected the amount of water maintained in the phloem cells of the main bole. At the same time, the dendrograph recorded the gradual seasonal increase in ring width as the wood cells were laid on by the cambium.

On the tree attacked by beetles, growth behavior was similar to that of the check tree until the attack was established. Person's (*U241*) report on this study stated:

> Early in June a very heavy attack was made and the tree was killed. This resulted in a rapid drying out and shrinkage of the phloem and sapwood which continued at a decreasing rate up until the end of the season. As the tree became drier and the needles ceased to function, the diurnal change in diameter became barely perceptible and the curve became almost a straight line.

The chart (fig. 32) illustrating the growth curve of this tree shows increasing diameter growth from May 5 to June 9. During the period a light attack occurred May 5 and a medium attack May 19. Neither of these attacks made any impression on the growth curve or the diurnal fluctuations in diameter. Following the heavy attack on June 9, shrinkage of the diameter began and was greatly accelerated from June 23 to July 14. After this the continued loss in diameter width was slight. The diurnal fluctuations were much less pronounced after July 21, but were still perceptible until September 23. It was Person's (*U241*) interpretation that the tree had been killed when the rapid shrinkage set in after the attack of June 9. This interpretation seems to be a sound one when a comparison is made of the growth curves of the attacked trees with those of check trees.

The Role of Micro-Organisms

The Blue-Stain Fungi

Soon after egg galleries are established by parent adult beetles, discolored areas appear on the surface of the sapwood and rapidly acquire a bluish-black color. They are caused by "blue-stain" fungi invariably associated with successful attacks of the bettles. Accord-

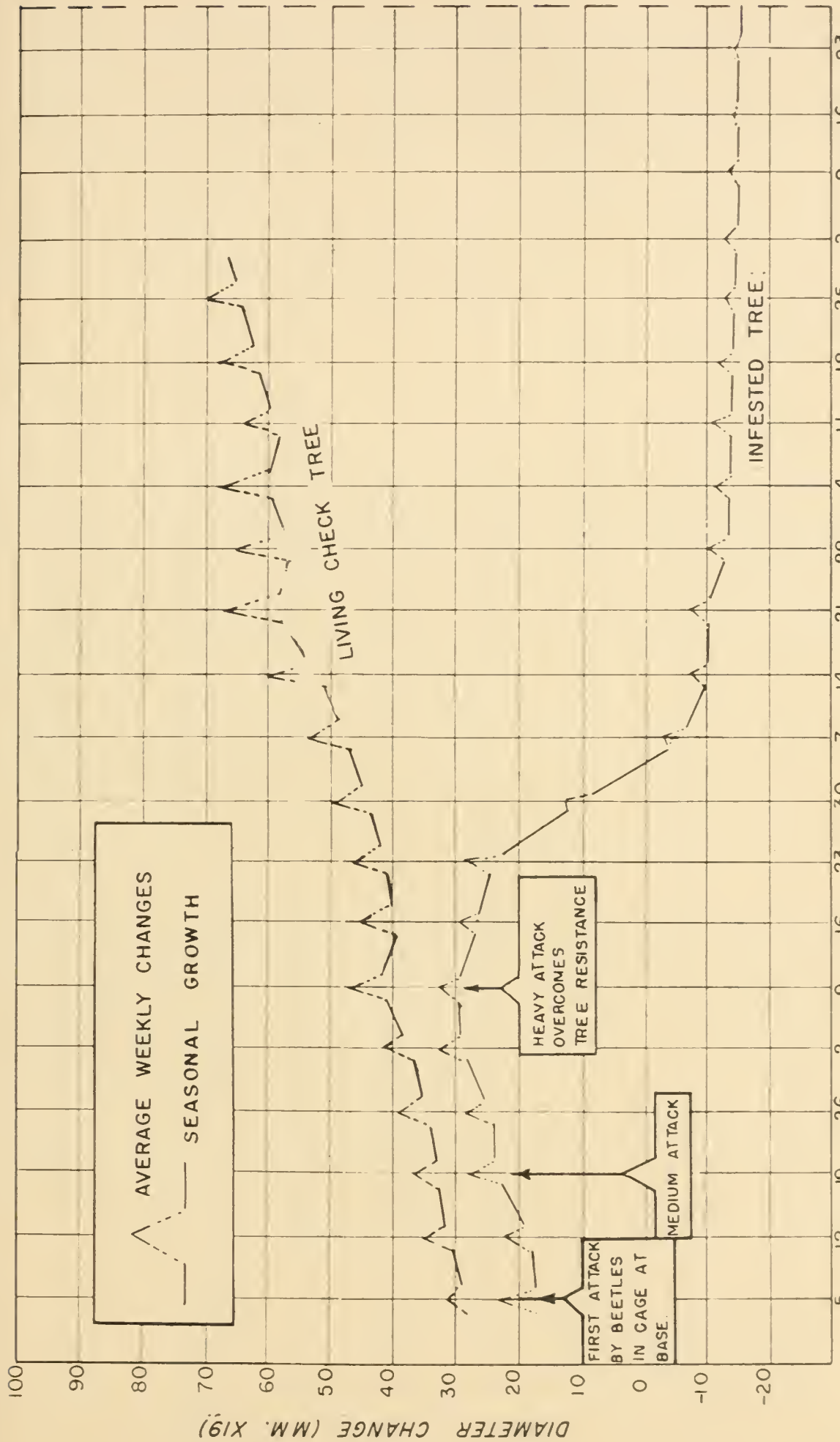

FIGURE 32.—Dendrograph records from living tree and tree attacked by the western pine beetle (*Dendroctonus brevicomis*).

ing to Rumbold (*115*): "The blue-stain fungus growing from the galleries of *Dendroctonus frontalis* [southern pine beetle] in eastern pines and of *D. brevicomis* in pines of California and Idaho has been identified as *Cerotostomella pini*." This fungus, which has been cultured from western pine beetle adults, is specific to the two bark beetles and is introduced into the trees at the time of attack, as shown by Rumbold's studies:

> Many fungi were isolated from the blue-stained wood of insect-infested trees, but as a rule only one fungus would be cultured from the stained area of a specimen collected when the tree had just been invaded by bark borers.

Parts of the Tree Attacked

Describing the general characteristics of this fungus, Rumbold (*115*) states:

> The fungus covers the wood beneath the bark with a black, granular looking growth, which makes the wood look as though covered with coal dust. The inner bark also shows this growth, mixed with particles of dried rosin. Beneath the black streaks the fungus grows in toward the heartwood. Hence the cross section of an infested sapwood branch frequently has the appearance of wedges of stained wood extending from the bark to the center . . . A microscopic examination of the wood shows that the fungus first invades the parenchyma cells of the wood rays. The hyphae pass from cell to cell through the pits. As their number increases the end walls of the ray cells are pushed out and later even the side walls are broken out by twisted strands of brown mycelium, which now fill the whole ray.

Relation to Brood Development

Blue-stain starts in the egg galleries of infested trees and usually occurs in irregularly distributed spots. If moisture conditions are favorable, it continues to spread through the sapwood and in time infects the entire cross section of sapwood. The heartwood, however, is not attacked. The increase in the volume of wood infected by the fungus is well correlated with the advance in brood development of the beetle. This relationship has been established by studies on a number of salvage logging operations where infested trees have been sawn into log lengths and graded.

A report by Salman and Johnson (*U285*) on 338 logs salvaged in 1935 by the Fruit Growers Supply Company near Susanville, Calif., summarizes the percent of mill degrade due to blue-stain according to brood stages at the time the trees were felled:

Brood stages:	*Logs (number)*	*Average blue-stain deduction (percent)*
Attack, parent adults, eggs, young to half-grown larvae	54	9.6
Young to full-grown larvae	52	23.7
Full-grown larvae, pupae, new adults, abandoned	232	47.1

Some blue-stain can be found in insect-killed trees as soon as successful bark beetle attacks are made. The percentage of sapwood blue-stained increases during brood development and reaches its peak about the time the trees are abandoned by the beetles. Usually

blue-staining of the sapwood is well developed by the end of the first season, and in general summer brood trees which dry out quickly have much less blue-stain than winter brood trees.

According to Wagener (*U315*) blue-stain is found in insect-killed trees even when salvage is rapid, but the stain percentage ordinarily is not high for the first two or three months after the initial primary beetle attack. The heartwood is not affected, but since it makes up only 40 percent of log volume in typical eastside ponderosa pine, the sapwood condition is the dominant factor in considering salvage.

Role of Blue-Stain in Rapid Dying of Trees

Craighead (*24*) advanced the theory that blue-stain fungus is responsible for the rapid dying of a tree after attack, more rapid than would be expected as a result of mechanical girdling by egg galleries. He suggested that this might be explained "by some toxic secretions of the fungi destroying the living ray tissues of the main stem or affecting normal functioning of the leaves in transpiration." In experiments with loblolly pine (*Pinus taeda* L.) Nelson and Beal (*101*) report that blue-stains inoculated into trees killed them without the aid of bark beetles, apparently by the complete blocking of conduction in the sapwood.

Caird (*16*, *U44*) found that the beetle's mining action alone is sufficient to desiccate the host. However, no work seems to have been done to determine whether the western pine beetle is dependent upon the action of the fungus to accomplish rapid killing of attacked trees. It is generally accepted that blue-stain does not attack and kill trees unless it is introduced by the beetle; on the other hand, it has not been demonstrated that the beetle can successfully attack and kill trees unless it is accompanied by the fungus. However, the association of the organisms is so constant and universal that the relationship appears to be more than accidental.

The Yeasts

Much less is known about the behavior and functions of yeasts associated with the attack of the western pine beetle. Person (*112*) first called attention to the probable role of a yeast considered to be a *Torula* (later determined as *Saccharomyces pastori* (Holst)):

> It was possible to make pure cultures of this organism, and some experiments were conducted on its fermenting capacity. Although some other yeasts, bacteria, and fungi were occasionally present in the cultures, the yeast was by far the most abundant and the only organism apparently always present on the larvae and new adults of the beetle. It was found that inner bark inoculated with this yeast was definitely attractive to the western pine beetle.

Struble (*U294*) looked for this yeast in the intestinal tract of the beetle. He cultured intestinal tracts of fully grown larvae in an agar-agar solution containing 10 grams of peptone, 2 grams of potassium phosphate, 0.5 grams of magnesium sulfate, 20 grams of agar-agar, and 1,000 cc. of boiled rice starch, with enough citric acid added to produce a pH of 4.8. All cultures produced a yeast. Struble concluded that "yeasts are evidently the normal organisms of the *Dendroctonus brevicomis* digestive tract, both in the larval and the adult stage of development. Fungi are occasionally present."

Holst (*40*) described a new species of yeast, *Zygosaccharomyces pini*, which was found associated with the western pine beetle from the Western States and the southern pine beetle from the Southern States. He also noted that "some anascosporous, mycelium-forming yeasts . . . were also frequently present." He was unable to find any evidence of direct relationship between the yeast and the beetle.[3]

Rumbold (*116*) does not mention any studies of yeasts cultured from the western pine beetle, but states that:

> The two types of yeasts, *Zygosaccharomyces pini* and the anascosporous yeasts, that were found regularly associated with *Dendroctonus monticolae* and *D. ponderosae*, are those found with other species of bark beetles. They appear to be widespread in the forests of this country. They are regarded as of secondary importance in causing the death of insect-infested pines.

Probable Function of the Associated Yeasts

Jeffrey (*U108*, *U109*) made a chemical analysis of the concentration of certain sugars in the inner barks of trees attacked by the western pine beetle and concluded that the changes that take place soon after attack are the result of yeast action:

> In recently felled trees, before attack, here is evidence of an increase of levulose and a decrease in sucrose. When trap trees are attacked by *D. brevicomis*, the reducing sugars in the inner bark, especially levulose, increase and the sucrose decreases rapidly. This is followed by a decrease in all sugars, which is especially rapid, close to the beetle galleries. The decrease is probably the result of abnormally high cell respiration, and of fermentation due to microorganisms introduced by the beetle . . . When a tree is felled or injured (and becomes attractive to the beetles) there is an increase of levulose and a decrease of sucrose such as would probably be associated with fermentation.

According to the small amount of information available, yeasts associated with western pine beetle attacks contribute to deterioration of a tree only to the extent of breaking down certain materials in the phloem as the tissues change from a living to a dying condition. The yeasts principal significance, as pointed out by Person (*112*), lies in the production of esters whose odors seem to attract the beetles.

Deterioration of Beetle-Killed Trees

Once the growth processes cease in a tree that has been attacked, changes set in that result in deterioration and ultimate decay. The foliage dies quickly and passes through a series of successive color changes; the dead needles finally fall and leave the limbs bare;

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[3] Further work was done in 1952 and 1953 by Moshe Shifrine, graduate student of the University of California, in cooperation with the Berkeley Forest Insect Laboratory, in regard to yeasts associated with *Dendroctonus* and *Ips*. The most common yeasts associated with the mountain pine beetle in ponderosa pine were *Hansenula capsulata, Candida sylvicola, C. parapsilosis,* and *Saccharomyces pastori* (*Zygosaccharomyces pini* Holst). In ponderosa pine, practically the only yeast found associated with the western pine beetle was *Saccharomyces pastori* (Holst).

woodborers and rots attack the sapwood and bring about its disintegration; the bark loosens and falls; and in the end the tree becomes a snag which may fall soon or may stand for years as a bleached "ghost tree." This chain of developments requires a period of years, and the various stages of deterioration correlate fairly well with elapsed time after the tree dies.

Color Phases of the Dying and Dead Foliage

The most easily visible effect of successful beetle attack on a pine tree is registered by the foliage in a succession of color changes somewhat resembling the color phases of broad-leaved trees as they develop autumn foliage. The presence of a bark beetle infestation in a pine area is easily recognized from a distance by the off-color appearance of infested and recently killed trees. Simply by viewing an area, an observer can gain an impression of the status and severity of an infestation. The interpretation of the color phases of beetle-killed trees has, therefore, been widely used as an index to bark beetle conditions in all detection surveys.

Terminology

According to Hopkins (*44*), "The first evidence of attack on living trees is the presence of pitchtubes on the trunks, mixed with reddish borings . . . around the base of the trees. Later the fading, yellowish, or reddish condition of the foliage is conspicuous evidence of the beetles' destructive work."

Hopkins was the first to define the color phases of infested trees, and these definitions have been commonly used in survey and control work. The term "tops" was used in connection with color terms designating the overall appearance of the crown.

Fading tops: noticeably paler green of the foliage.

Sorrel tops: the yellowish foliage of trees dying from attack.

Red tops: color of the foliage after the tree is dead and usually after the broods of destructive beetles have emerged from the bark. This reddish brown of the adhering pine needles may prevail for a year or more after the trees are dead.

Black tops: condition of dead trees after all of the needles have fallen and 2 or more years after the beetles have left them.

Relation of Color Phases to Brood Development

Keen (*U132*) found a certain amount of correlation between the development of color phases of foliage and the various stages of brood development in bark. He also found that these relationships varied considerably with the time of year. He illustrated the relationships by graphs, with the following general summary:

Fading: In general a tree fades soon after the eggs hatch and at about the time the larvae enter the outer bark. Trees of the overwintering generation, however, do not fade as a rule until the first warm weather in spring, and before pupae form.

Sorrel: As a rule trees turn sorrel at about the time of maximum pupation or the first forming of the new adults.

Red: Trees generally turn red about the time of maximum emergence of the beetles.

Black: Completely abandoned by the western pine beetle; wood borers and secondary insects beneath the bark and in the wood.

Deterioration of Foliage

In 1933 Buckhorn (*U37*) charted the change of color phases for a series of trees attacked during the previous year in the Ochoco area in east central Oregon. He showed that up to the last of May 1933 90 percent of the 1932 first-generation trees were sorrel, the remainder still green. For the partial 1932 second generation trees, 70 percent were fading and 30 percent were still green. For the partial 1932 third generation trees, only 40 percent had faded. During June and July, the color phases in all trees advanced rapidly, and by November 1 practically all had reached the red and dull red stages. After the first of September, the loss of needles was noticeable, and the trees went into the second winter with about 65 percent of their foliage.

The red color phases may be broken down into "bright red" and "dull red"; bright red identifying trees that have been attacked and killed during the current year, and dull red applying to the weathered appearance of needles that have passed through a winter.

The red phases last for a prolonged period, the length depending somewhat upon weather conditions to which the abandoned trees are exposed. Winds and sleet hasten the fall of dead needles. The red-phase period varies with locality and region, but in general there is a progressive fall of needles after the first year with some trees retaining 10 percent or more of needles for a period up to 5 years (*U79*).

In 1935 Keen (*78*) surveyed four 640-acre sample plots in southern Oregon with a total of 3,320 trees killed in 5 years. His records showed 15 percent of the trees with needles fallen after the first year; 38 percent after 2 years; 62 percent after 3 years; 94 percent after 4 years; and 99 percent after 5 years. In general, if all trees with red needles are counted, they average 1.8 years of loss.

After dead trees have dropped their needles, they are considered to be in the "black-top" stage, even though a few weathered, inconspicuous brown needles remain. Snags in the black-top phases, before bark has started to fall, may be from 1 to 13 years old. A count of all such snags plus red-tops has been found to average about 6.7 years of loss.

Snags of the next older class, where the bark has started to fall, are called "yellow-tops." They may be aged from 2 to 15 years or more. Studies have shown that a count of yellow-tops plus black- and red-tops will average about 8.3 years of loss.

Snags of the oldest class, with most of the bark fallen and the wood bleached gray white, are called "white-tops" or "buckskins." Counts show these snags are aged from 5 to 30 years or more. A count of all snags including red-, black-, yellow-, and white-tops equals about 9.6 years of loss. In cruising timber of the interior ponderosa pine type, a rule of thumb has been used for some years in assuming that a count of all snags is equal to about 10 years of loss.

On the whole, the early fading and sorrel stages are of greatest significance in appraising current bark beetle infestations in survey and control operations. Beyond these stages, trees are mainly abandoned and the red and black phases are of importance only in estimating past losses.

Falling of Bark

The falling of bark has been used as an indicator of the rate of deterioration of a beetle-killed tree. Hall (*U79*) states that there is comparatively little loss of bark up to the fifth year after death; at the eleventh year the average loss of bark is approximately 50 percent, and at the sixteenth year the loss is approximately 90 percent.

From recruising a series of 640-acre sample plots in southern Oregon, Keen (*78*) found that the rate of bark falling was exceedingly variable. Trees with all bark intact might be aged from 1 to 13 years and average 5½ years; with bark beginning to slough, they might be aged 2 to 15 years or more and average 11.2 years; with more than 75 percent of bark fallen, they might be aged from 5 years with the average about 25 years.

Deterioration of the Main Bole

The combined action of weather, insects, and fungi is responsible for the disintegration of sapwood and heartwood that occurs gradually after a tree has been abandoned by bark beetles. Some study has been given to the causes that bring about this decadence, because the rate of deterioration is important to the possibility of utilizing the lumber values in beetle-killed trees.

Influence of Weather Factors

The role of weather in the deterioration of bark and wood has not been studied, but its effect cannot be altogether disregarded. Climatic conditions regulate to a considerable extent the amount of water in the wood of dead trees. Rots depend upon this moisture for favorable conditions for development. Beetle-killed trees in moist sites appear to rot rather quickly, while those found on dry sites have a tendency to check because of rapid drying out. Both conditions destroy the merchantable quality of the wood and are factors in the process of decadence.

Insects

Since the western pine beetle does not penetrate the wood, it is only indirectly a factor in the deterioration of the main bole. Several species of wood boring insects, however, do attack beetle-killed trees, bore into the wood, and introduce associated rots that assist in the disintegration process.

Ambrosia beetles.—While the lower trunk of the freshly killed tree is still fairly moist, the sapwood and later the heartwood are invaded by ambrosia beetles or "pin-hole" borers. These beetles plant fungi in their galleries to feed their larvae. Holes made by

these beetles apparently admit other spores of wood-rotting fungi and hasten wood decay.

Trypodendron ponderosae Sw. is one of the most common ambrosia beetles found attacking the base and lower 8 to 10 feet of the trunk of beetle-killed ponderosa pines that are moist or show "sour sap" at the base. According to Buckhorn (*U37*), the galleries penetrate the sapwood and heartwood and branch considerably. These beetles ". . . attack the trees soon after they are killed by bark beetles and continue until late in the fall and start again with favorable spring temperatures. Brood was found overwintering in the adult stage mostly in the newly formed galleries, but a few were wintering in the old brood trees and at the base of trees under loose bark scales." Scattered emergence occurred from April to August, but peak emergence was from October 2 to December 7. Apparently there is only one generation a year.

Gnathotrichus retusus (Lec.), another common species of ambrosia beetle found breeding at the base of moist ponderosa pines, makes numerous small pin holes in the sapwood. The galleries usually have one or more horizontal branches following an annual ring, and from these larval "cradles" are constructed both above and below. The brood overwinter in the adult and larval stages in both old and new beetle-killed trees. Adults are also found hibernating at the base of trees under loose bark scales from the ground line to several inches below ground and on the roots. Emergence begins in April and continues spasmodically until November. Other species of ambrosia beetles may occasionally be found doing similar work.

Xyleborus scopulorum Hopk., another pin-hole borer, is found in beetle-killed trees after the sapwood becomes rotten and punky. This species makes no cradles, but frequently constructs branched horizontal galleries in which the larvae work end to end.

Sapwood weevils.—Within a year, small black weevils (*Cossonus ponderosae* V.D. (6 mm. long) and *C. crenatus* Horn (5 mm. long)) are found under the bark of killed trees. They usually work in blue-stained sapwood. The small, white, curled larvae make small, round, mostly horizontal pin holes in the sapwood to a depth of 3 inches.

Rhyncolus oregonensis Horn. are small, dark, reddish-brown weevils, 4 mm. long, found under the bark soon after a tree is killed. The adults construct galleries radially and horizontally deep in the sapwood. Ten or more adults may be found in a single gallery working side by side, particularly in very dry wood.

Round-headed borers (*Cerambycidae*).—Several round-headed borers are attracted to ponderosa pines recently killed by the western pine beetle. When the eggs of these borers hatch, the larvae start penetrating the sapwood and heartwood.

Asemum represented by three species, may be found in the larval stage mining the moist sound sapwood and extending their oval mines into the heartwood of trees dead from 2 to 7 years or more. The galleries in the wood are usually packed with red frass, except for the pupal part which extends to near the surface of the bark. *A. mokelumne* (Csy.) is the species most commonly found in the wood of ponderosa pine. *A. atrum* Exch. bores in many species of

conifers including ponderosa pine. *A. nitidum* Lec. is a larger species which does similar work.

Ulochaetes leoninus Lec. may be found laying eggs on ponderosa pines a year after trees have been killed. The larvae usually work in the wood for many years, particularly at ground line and in the roots. The larval borings by this species are important in undermining pines and causing them to fall.

Ergates spiculatus Lec. is a large wood borer whose larvae may be found in the sapwood and heartwood within 3 years after death of ponderosa pines. It continues to work in old trees and stumps until the wood is completely riddled. It makes very large oval tunnels, an inch or more in largest diameter. This is one of the most important insects in weakening the heartwood and causing trees to fall.

Strangalia plagifera (Lec.) larvae work in the outer 4 inches of old decaying sapwood of ponderosa pine. Pupae form in cells 3 inches under the surface. This species is common in the older pine snags.

Many other species of roundheaded borers may also be found in old decaying wood of beetle-killed pines, and are important in contributing to deterioration of the main bole.

Flatheaded borers (*Buprestidae*).—A few species of flatheaded borers are also found working in beetle-killed pines.

Chalcophora angulicollis Lec. is a large species that lays its eggs on the bark of dead pines about 2 years after the trees are killed. The larvae bore into the sapwood, and will be found working from the surface of the wood into the heartwood and down into the roots for as long as 5 years after the tree's death.

Buprestis aurulenta L. works in the pitchy wood of fire scars and at the base of old snags. The larvae develop slowly and may be found infesting this wood for many years.

Other flatheaded wood borers include *Buprestis laeviventris* (Lec.) and *Dicerca tenebrosa* (Kirby).

Other wood borers.—Rushia californica (Fall) is a common species of wood borer found under the surface of hard, dry sapwood of snags over 2 years old. The larvae are narrow, white, about 12 mm. long with two prominent hooks on the rear end. They make small, flattened, oval mines running vertically in all directions. Partly filled with powdery boring dust and partly open, the mines occur down to but not below the surface of the ground.

Phellopsis porcata (Lec.) adults are large, rough, brown beetles. Larvae make long winding vertical tunnels packed with frass in the wood of snags 3 years or more old.

Termites.—The dampwood termite (*Zootermopsis nevadensis* (Hagen)) commonly attacks the damp sapwood of pine snags. Also a subterranean termite (*Reticulitermes hesperus* Banks.) is often very active in destroying the sapwood of old beetle-killed pines. It also continues into the heartwood of the older snags.

Fungi Causing Stain and Decay

Wood-staining fungi include the blue-stains *Cerotostomella pini* and others, and a yellow stain of an undescribed fungus studied by Wagener (*U315*). Wagener reported that blue-stain would be found

in insect-killed trees even though salvage was rapid, but that the stain percentage ordinarily was not high for the first 2 or 3 months after initial primary beetle attack. In southern Oregon, Patterson (*108*) found that the amount of blue-stain varied in individual trees according to the amount of sapwood, which in general was 40 percent of the merchantable volume of beetle-killed trees. During the first season after attack, deterioration of lumber values in the tree was confined chiefly to a degrade due to bluing of the sapwood.

Wood that has been blue-stained retains much of its structural properties and can be utilized, but because of discoloration it is graded much lower for commercial uses than noninfected lumber. Under some conditions, however, blue-stained wood for special uses has been able to command high prices.

Sap rot.—Wagener (*U315*) found that wood-destroying fungi (unidentified) may gain considerable headway in the sapwood of ponderosa pine during the first year after the tree is attacked: "Once established the decay appears to develop rather rapidly from narrow longitudinal streaks into irregular patches. The extension takes place along the surface of the sapwood, no doubt aided by the activities of secondary insects under the bark. From here it spreads somewhat more slowly and irregularly toward the heartwood."

Fomes pinicola, the red belt fungus, is the most common cause of rot in insect-killed ponderosa pine. It first appears in the sapwood as a faint yellowish or brownish stain. In the advanced stage it reduces the sapwood and heartwood to a light reddish-brown, crumbly mass that has a tendency to fracture into cubes. This rot is an important factor in the ultimate decay of beetle-killed snags.

Polyporus volvatus develops in the outer sapwood while western pine beetle broods are still in the tree. Its fruiting bodies develop thorough emergence and ventilation holes after the beetles emerge, and are most plentiful during the season following emergence. This fungus causes a soft grayish rot of the sapwood which often progresses very rapidly.

Progress of combined rots.—In 1922 Boyce (*7*) made a study of deterioration of treated trees on an insect control project near Klamath Falls, Oreg. He found that while the heartwood of ponderosa pine resisted rots much longer than the sapwood, it also decayed in time:

> Deterioration is very rapid and is caused by decay, particularly the very rapid decay of the sapwood followed more slowly by the breaking down of the heartwood. The resulting loss is so high by the end of the second season that felled trees must be utilized by the beginning of this time or else the volume of merchantable wood is so small that it is of little commercial importance.

Boyce found that the cull 2 years after the trees were killed amounted to 60 percent; this percentage increased progressively with each succeeding year until by the seventh year 92 percent of the wood was valueless.

Patterson (*108*) reporting on a 1928 salvage operation of beetle-killed ponderosa pine on Modoc National Forest in California, showed the following percentage of merchantable volume salvaged, by seasons:

Season of attack:	*Blue-stained wood (percent)*	*Salvaged in 1928 (percent)*
1927 winter brood	43	100
1927 summer brood	39	86.4
1926 winter brood	37	73.2
1926 summer brood	50	47.7

No tree dead longer than 2 years contained enough merchantable stock to defray expenses of logging.

Brundage and Orr (*12*) discussed the selling values of lumber obtained from infested trees salvaged on an eastside pine area in 1935.

How Long Beetle-Killed Trees Stand

In the processes of deterioration, wood of beetle-killed trees breaks down, particularly at the ground line; the snags finally fall; and their ultimate disintegration takes place on the ground. Keen (*65*) made a study in 1928 of the time these beetle-killed trees remained standing on one 640-acre sample plot in Modoc County, Calif. He supplemented this early study in 1932, 1935, and 1949 by a recount of snags still standing on a number of additional 640-acre sample plots in the Klamath Basin of southern Oregon (*78*). He found that the natural falling of ponderosa pine snags in this part of the pine region follows a rather consistent pattern (fig. 33).

Fully 85 percent of beetle-killed snags remain standing at the end of the first 5 years. Then as the butts become riddled with wood borers, termites, and wood rots, the trees fall at a rapidly increasing rate. The bulk of the snags go down between the fifth and twelfth year after trees have been killed. At the end of 10 years, about 40 percent remain standing. After the twelfth year, the rate of

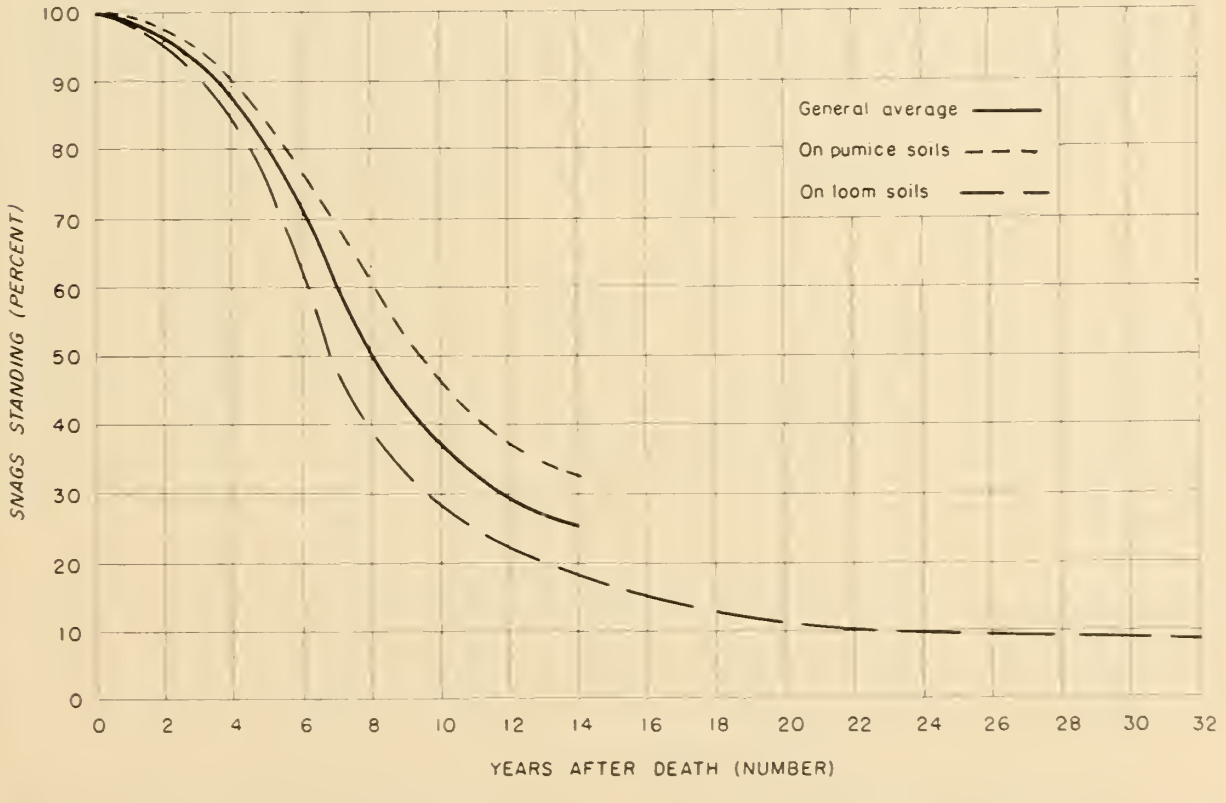

FIGURE 33.—Percent of beetle-killed trees remaining standing as snags for 1 to 32 years after death.

snag fall slows down and the more resistant snags of larger diameter remain standing for many more years. Ten percent of snags 17 to 30 years old were found still standing when the Modoc plot was recruised in 1949 including 28 percent in the 40 inch and over d.b.h. class. It was found that snags stood longer on dry pumice soils than on the more moist clay and loam soils.

It is a common observation that trees with pitchy butts, those standing on dry sites, and those charred and "case-hardened" by fire are the last to succumb to decay. Studies of snag falling show that these make up the last ghost trees still standing in areas where epidemic infestations occurred years before.

HOST TREE RESISTANCE AND SUSCEPTIBILITY

There are two opposing theories as to how western pine beetles find suitable host trees to attack. One theory, advanced by Person (*112*), is that certain susceptible trees emit odors or other attractive substances that draw a few beetles to begin an attack. This attack, in turn, sets up additional attractive influences, and these bring in additional beetles to assist in overcoming the trees.

The other theory, advanced by Callaham (*U48*, *U49*) is that the attack on trees is merely a random chance, at least as far as the first beetles are concerned. Callaham believes that beetles flying through the woods attempt to attack many trees. On resistant trees, these attempts fail because of high quantity of oleoresin, and the attacking beetles are pitched out. But on a susceptible tree, little or no resistance is offered, and the attacks succeed. Once the initial attacks are started, other beetles are drawn to the scene until the tree is overcome. The tree initially attacked becomes a focal center, and beetles may continue to be attracted until a group of trees is killed around this first or "key" tree.

Neither of these theories has been demonstrated. However, it is known that certain trees are more susceptible to attack than others, regardless of how the beetles happen to find them.

Relation to Tree Conditions

Physiological Factors

The capacity of the tree to maintain its vital physiological functions during attack by beetles provides an important measure of the tree's resistance. Consequently, growth and other physiological conditions of the tree have been studied in detail.

Growth

From 1924 to 1928 Person carried out a series of studies to determine whether the mortality of pines from western pine beetle attack was related to such factors as growth rate, quality of site, tree diameter, and size of crown. He considered growth only as it was expressed by ring-width measurements (average ring width in last inch of radial growth) in basal increment cores. Such cores from beetle-killed and living trees were collected by Person from the west-side type of the Sierra National Forest, Calif.

A similar large series of cores was collected and studied by Keen from survey plots representing eastside type in southern Oregon and northern California. The growth rates were measured and compared between trees of the same diameter growing on the same sites. The results of these studies were reported by Person (*111*, *U237*, *U242*). who concluded that there is a definite selection by the beetles of the slower growing trees. Comparison of attacked and unattacked trees of the same diameters on the same sites, showed that the beetles selected the slower growing trees in 75 percent of the cases. In 91 percent of the trees attacked, the basal radial growth rate was below 2 mm. annually.

Struble (*U303*) further confirmed the relationship of tree growth and beetle attack on the Sierra National Forest, Calif. For 230 trees that died during the period 1917–26 out of a total stand of 1,362 trees, the selection by growth class favored the slow-growing trees (fig. 34).

Craighead (*21*), Miller (*92*), Person (*111*), and others (*26*) all reported that the slower growing trees were most frequently killed by the western pine beetle. What these authors meant by "slow growing" was not defined. However, the observations and data upon which these statements were based dealt only with the basal radial increment of the main trunk.

These early studies were followed by a large number of increment-core growth studies in this and other areas. In 1924 Keen began the collection of increment cores from both live and beetle-killed trees of different ages, growth rates, and conditions of crown vigor. This led to the development of his ponderosa pine tree classifica-

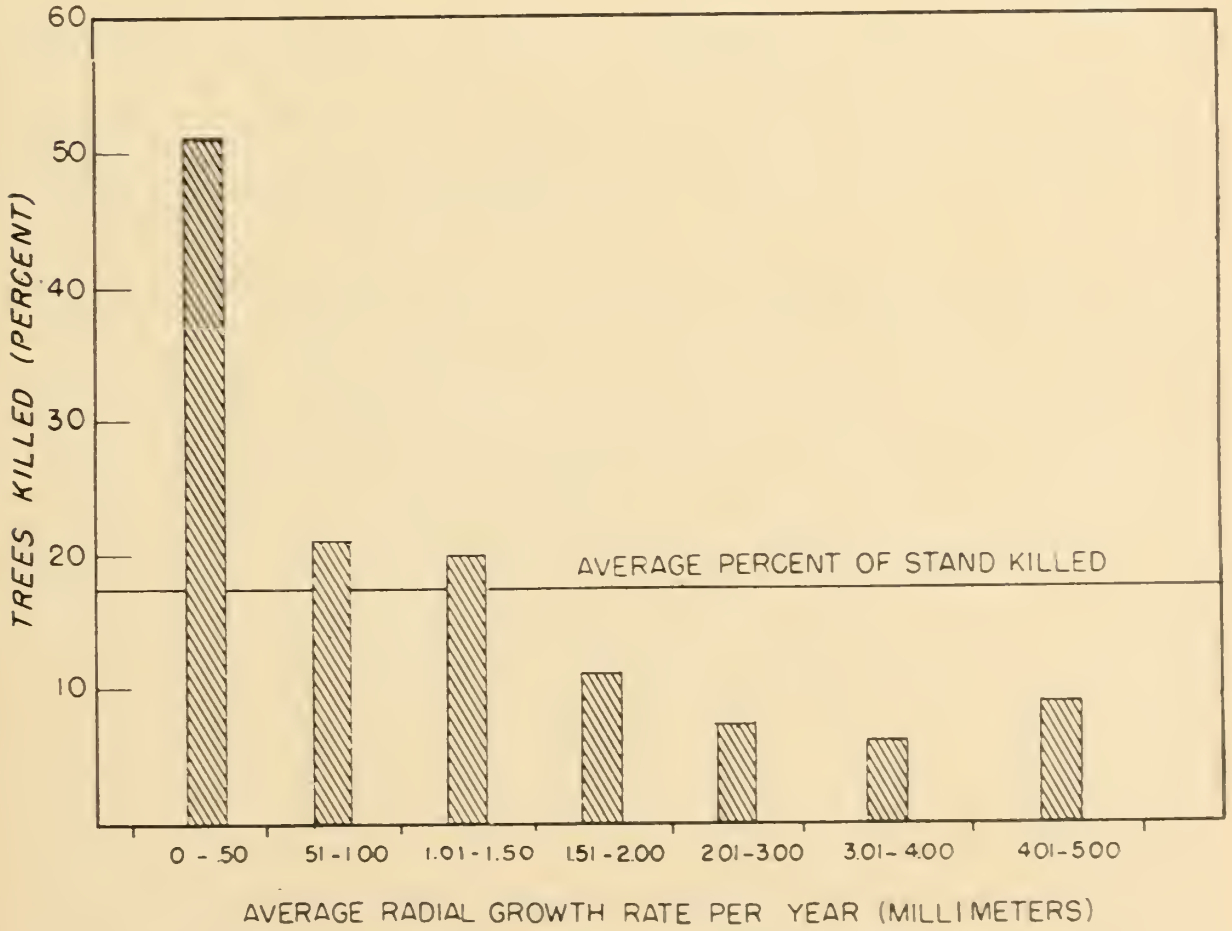

FIGURE 34.—Percent of trees killed in relation to average radial growth rate per year, Cascadel area, Sierra National Forest, Calif., 1917–26.

tion as a guide to susceptibility to western pine beetle attack (*68*), and to an analysis of tree growth rates and weather cycles in eastern Oregon (*69*). The study showed that radial growth was correlated with precipitation, and that drought conditions and slow tree growth during the period 1917–37 were undoubtedly important factors contributing to heavy timber losses from the western pine beetle during this period.

The resistance of vigorous, fast-growing trees to western pine beetle attack has been demonstrated not only by the lack of susceptibility of young and dominant trees under natural forest conditions but also by caging experiments in which attempts have been made to kill the trees by induced attacks of the beetles.

Miller (*U193*) describes an experiment on the Sierra National Forest in 1925 which involved forced attacks by the western pine beetle on two trees of widely contrasting growth rates. The basal 10-foot part of each trunk was enclosed in a screen cage and quantities of infested bark placed in each cage so that emerging beetles were forced to attack the tree. The results were as follows:

Item:	*Tree No. 1 (fast growing)*	*Tree No. 2 (slow growing)*
Diameter breast high	36 in.	28 in.
Height	120 ft.	110 ft.
Crown class	Dominant	Intermediate.
Crown form	Pointed	Flat.
Crown length	Long	Short.
Number rings in last inch of radial growth.	5	64.
Width of 1924 ring	2.30 mm.	0.25 mm.
Total number adult beetles emerging in cage August 27–September 20, 1925.	14,559	8,373.
Attack on bark surface within cage August 27–Sept. 20.	430	645.
Attacks outside of cage for 2½ feet above cage top.	20	175.
Final result	No attacks on mid- or upper bole. Tree survived.	Entire bole attacked. Tree succumbed.

The slow-growing tree was attacked and killed, and enough non-caged beetles were drawn into the area to attack and kill two adjacent trees. The great force of beetles liberated in the cage for the vigorous tree (No. 1), however, was unable to overcome the tree's resistance and also failed to attract beetles above the cage.

The following year, Person (*U238*) carried out similar tests on a more extensive scale. Another attack was forced on the same fast-growing tree (No. 1) with the same result—the tree still resisted the beetles and suffered no apparent setback in growth as a result of the attack the preceding year. In addition, Person caged four more trees—one rated fast growing, one medium, and two slow. In this test all four of the trees were successfully attacked and killed by the beetles. However, it required more beetles a longer time to kill the fast-growing tree than the slower growing ones. Person pointed out that "the period between the first attack and the date on which the tree was overcome was over twice as long for the fast-growing tree." Also, "the amount of pitch given off in resisting

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FIGURE 35.—An 18-foot cage used to force western pine beetles to attack a fast-growing ponderosa pine. Cascadel Experiments, 1926.

attacks was over twice as large on the basal 3½ feet of the fast-growing tree (fig. 35) as on the slow-growing ones." Person concluded from these experiments that:

> Yellow pine trees vary in their resistance to *D. brevicomis* attacks. The data so far secured indicate that the resistance of a tree varies roughly with the growth rate; other conditions being equal. The fast-growing trees offer the most resistance, the slow-growing trees the least. Very fast growth, thick bark, and large heavy crowns are evidently associated with this resistance.

Keen (*U142*) analyzed the variation in average number of western pine beetle attacks per square foot of bark surface with growth rates of ponderosa pine on the Jenny Creek area of southern Oregon during the 10-year period 1917–26. He found a direct correlation between number of attacks and radial growth (fig. 36). When the growth ring was narrow for a certain year, fewer beetles attacked the bark surface; when the growth ring was wide, more beetle attacks per square foot were required to kill trees. This indicates that vigorous growth of trees produces resistance to bark beetle attack.

The relationship between growth rate and selection is not fixed but varies according to intensity of infestation and availability of

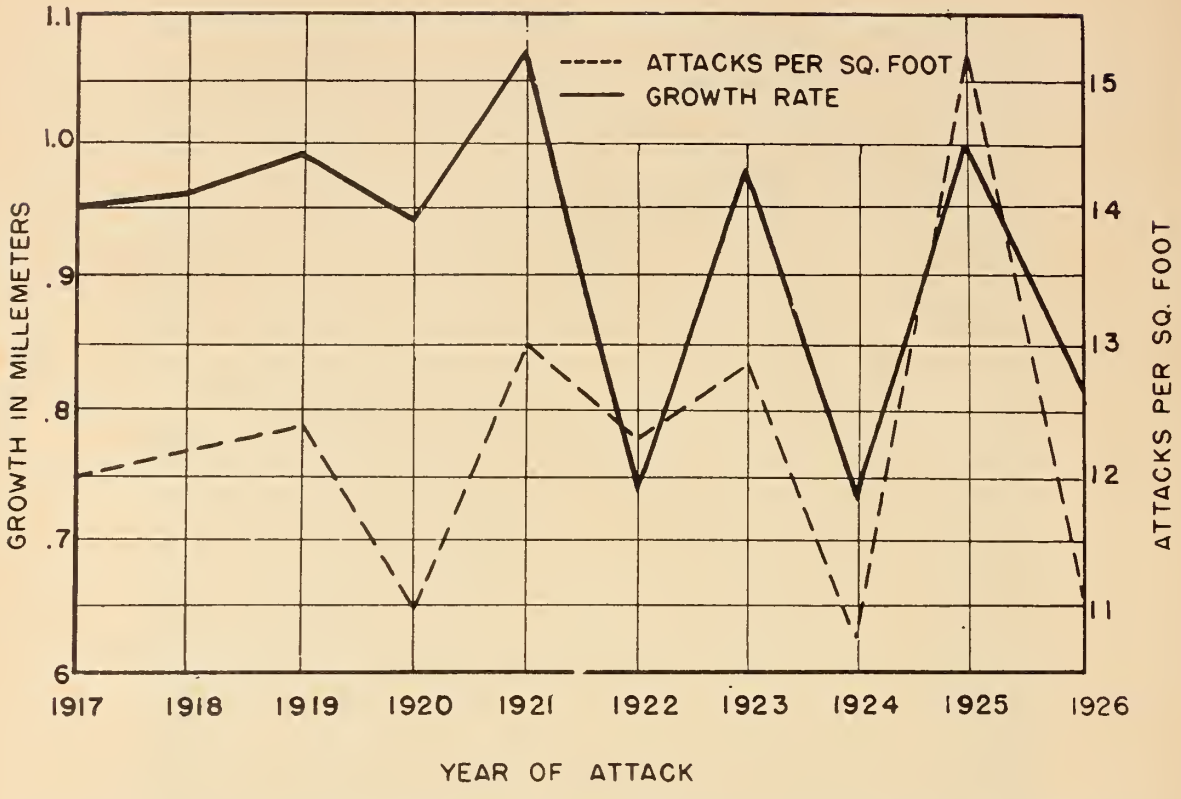

FIGURE 36.—Number of attacks per square foot of bark surface in relation to average annual radial growth of ponderosa pine. Jenny Creek Area, southern Oregon, 1917–26.

slow-growing trees in a stand, as indicated by further work by Person in 1927–28. This was expressed in Person's report (*U242*):

> The degree of selection exercised by the western pine beetle evidently depends upon the ratio of beetle population to the number of slow-growing susceptible trees. . . . An increase in the number of such trees tends to increase the infestation, a decrease in the number tends to decrease the infestations. A continued supply of very slow-growing trees usually results in an epidemic such as occurred on the Modoc area. But if after a large (beetle) population has been built up and the number of susceptible trees is reduced, then trees of fairly fast growth will be killed until the beetle population is also reduced by the resistance of the fast-growing trees.

Persons found that the highest degree of selection occurred when the infestation was at a low and fairly static stage. As an infestation increased, the degree of selection decreased. The least selection was found to occur just after the peak of an epidemic when the infestation was starting to decline. At this point, the beetle population was still high and the number of slow-growing, highly susceptible trees was relatively low.

An illustration of this tendency of the beetles to become less selective during epidemic periods is found in the 22-year record of the 80-acre Cascadel tree selection plot on Sierra National Forest, Calif. In 1932 and again in 1942, Struble (*U303*) analyzed growth conditions on this plot and found substantial differences in the growth rate of beetle-killed trees during endemic and epidemic infestations. His conclusions, illustrated by figure 37, were:

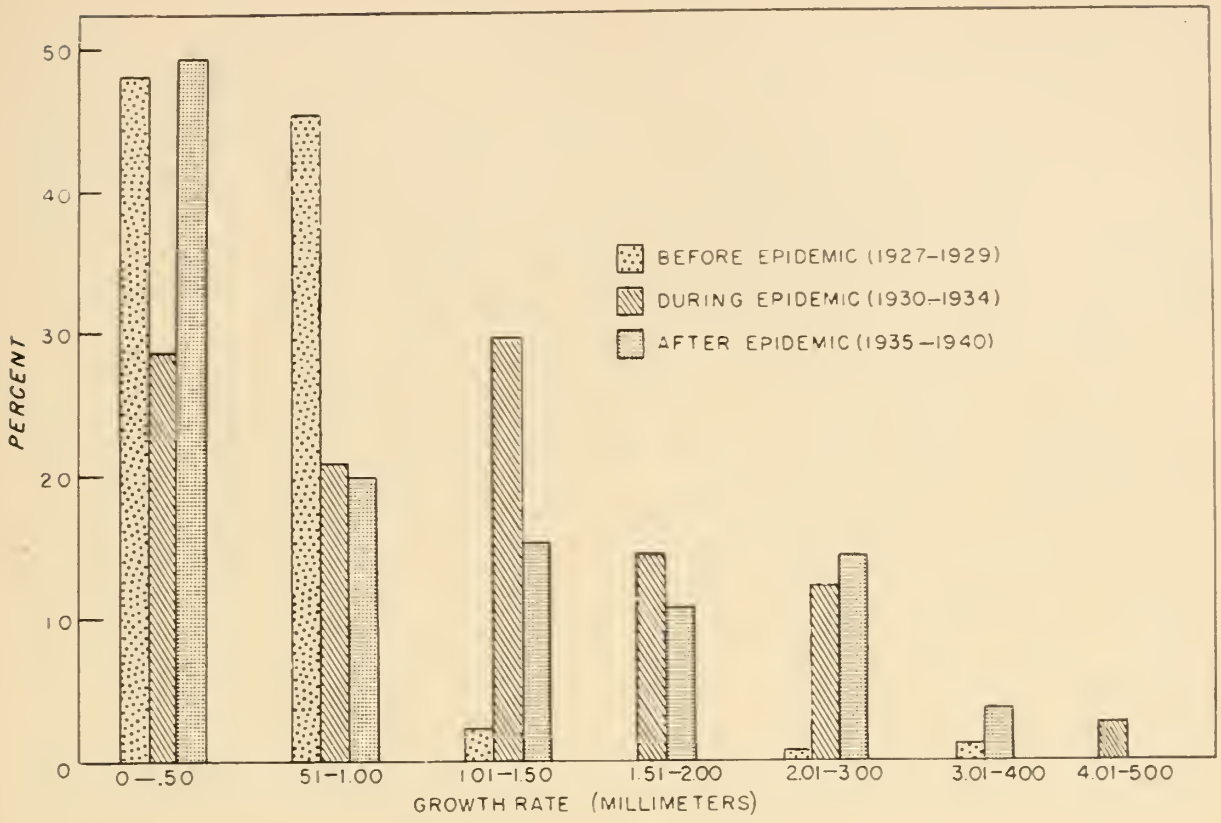

FIGURE 37.—Growth rate selection by western pine beetles before, during, and after an epidemic.

Under endemic conditions on the plot (1918–27), slow-growing trees were selected by the western pine beetle in the greatest percentage of cases; most of those killed were growing less than 1.00 mm. per year in average radial increment for the 10-year period prior to death.

This preference was diminished during epidemic years (1930–34) when there was a distinct tendency for the beetles to attack faster-growing trees; moderately growing trees (average 1.9 mm.) were selected more often than the slower-growing trees.

The return of endemic conditions (1935-40) was accompanied also by a gradual return of selection preference for slower-growing trees.

In 1940 Salman (*U279*) made a study on Modoc National Forest. California, of radial growth in relation to mortality of high-risk trees. His study considered not only current rate of growth in high-risk trees, but also length of time such trees had been in a slow-growing condition. Salman's conclusions were:

1. The types of trees in which most of the loss has been recorded, i.e. high-risk trees, are generally the slower-growing ones.
2. The slow growth rate is of recent origin and probably temporary, to be terminated either by death or recovery.
3. Growth abnormalities (missing rings) tend to occur more often in the high-risk trees.
4. No apparent relation was found between crown characters used in rating risk and any particular type of growth pattern.

In 1940–41 Keen analyzed growth conditions from increment cores taken from survey plots in eastern Oregon. He found (*U158*) that "a 15-core sample from 'index trees' (Class 2A or 3A) on a

given plot gives a reliable basis upon which to compare relative annual growth differences between plots." The maximum error of the mean from such a sample was approximately 16 percent. Another study (*U157*) compared the long-term growth rate before death in beetle-killed trees with the rate in living check trees; it also compared the growth in different age and vigor classes of Keen's tree classification (p. 177). From this study of radial growth measurements from 550 trees, the following conclusions were reached:

1. Growth patterns of beetle-killed trees were similar to those of living trees, except that on the average beetle-killed trees were much more complacent in their growth and this characteristic was evident for fifty years or more preceding death.
2. The growth rate of beetle-killed trees is much slower than the general average of living trees in the stand, and this inferior growth rate has been characteristic of such trees for a long period of time. In this study, beetle-killed trees on the average were found to be growing less than 0.7 mm. per year during the past thirty years. (Fig. 38.)
3. Susceptible tree classes were found to be growing on the average more slowly than the average beetle-killed trees in the decades preceding 1910, while the resistant tree classes were found to be growing at a faster rate. In the decade preceding death, growth of the beetle-killed trees was further reduced to the minimum of any tree class (4C).
4. Within any tree class, the beetle-killed trees were found to be those growing more slowly than the average of that tree class.
5. A general retrogression in growth rate of trees killed during 1940, more pronounced than in living trees, started in 1917.
6. Death was preceded by 5 years of rapid growth decline in opposition to the growth trend of trees that lived.
7. Except for the change in growth rate, nothing was found in the pattern of beetle-killed trees which would be helpful in dif-

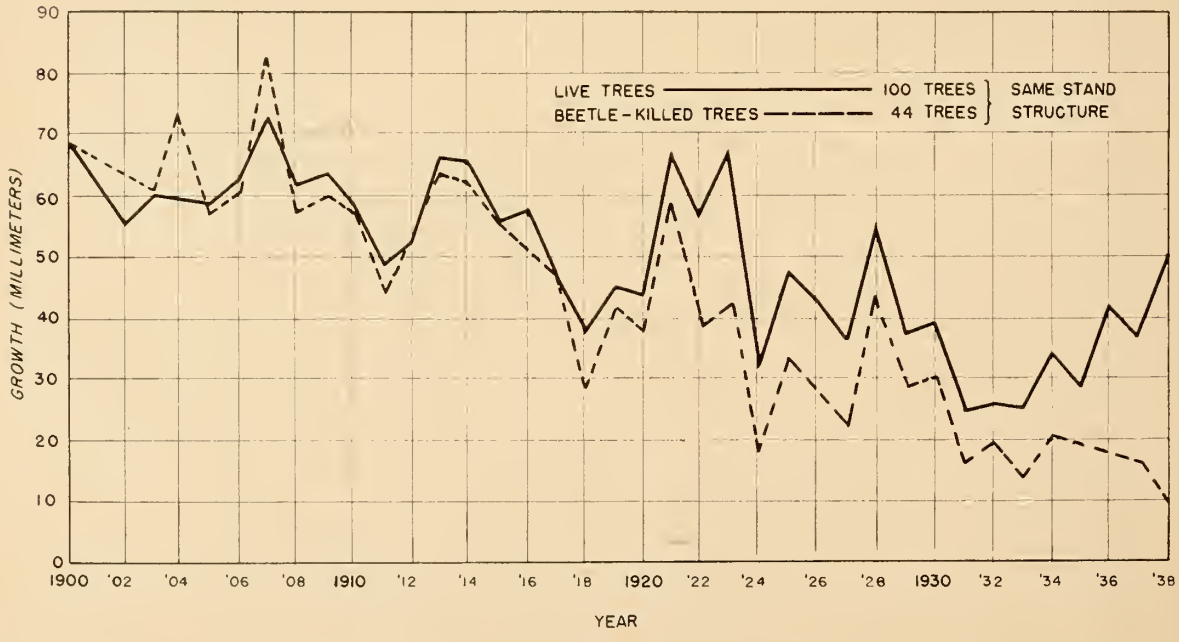

FIGURE 38.—Annual radial growth comparison between live and beetle-killed trees 1900–1938, Goodlow Mountain Plot, Fremont National Forest, Oreg.

ferentiating them from other slow-growing trees of susceptible tree classes.

Of the general application of the results of this study to practical use in the marking of high-risk trees, Keen commented:

> There is little hope for using radial growth characteristics for field determinations of high-risk trees or in picking trees which are about to die by a field examination of increment cores, even though this is a fairly reliable indicator of changes taking place in a tree's vigor and its resistance to insect attack.

It was not until 1942 that Bedard (*U15*) raised the question of what constitutes a reliable measure of growth vigor. Commenting upon previous studies on the relation of tree growth to resistance and susceptibility to beetle attack, Bedard stated:

> The radial growth of trees has long been used as a standard measure of tree vigor and its response to various environmental factors. However, the physiological concept of growth in woody plants considers four main meristem regions which produce vertical elongation of the main axis, horizontal expansion through branching, secondary thickening, and leaf development. This places the main meristems in *Pinus* at the shoot tips, near the root tips, at the cambium, and at the base of the needles.
>
> As far as could be ascertained, most of the work which has been done with tree growth deals with the activity of a single, or at most two, growing regions. Only one case could be found in which the worker studied all four meristems at the same time. Leader elongation and cambial growth have been most frequently investigated, but only rarely have measurements of both of these activities been recorded simultaneously for the same individual.

By applying different nutrients and water to the soil, Bedard (*U21*) was able to show differential effects in the various meristems of young pines. He concluded that the different soil treatments, compared with untreated trees, showed "the inadequacy of any one meristem as an indicator of tree vigor. Needle development, considered as to weight, length, and complement, appears to be the best single indicator of vigor."

Conduction

Studies by forest entomologists on the relation of conduction to susceptibility have been largely incidental to studies of the disturbance of this function caused by the action of blue-stain and of insects associated with the western pine beetle. However, studies have been made of conduction in high-risk ponderosa pine by West (*U329*). Salman and Johnson (*U288*), and Patterson (*U228*).

West's first studies, carried out on Modoc National Forest in 1938, sought to determine whether the wood of high-risk trees could be preserved before beetle attack by injecting copper sulfate into the sap stream. The first difficulty West met was the ineffective distribution of chemicals because of failure of the conductive system in most high-risk trees. Conduction of the chemical was erratic and followed limited channels through the sapwood layer. Patterson

encountered similar difficulties in later attempts to introduce preservative chemicals into high-risk trees by the saw-kerf method. Results of these experiments indicate that in high-risk trees the conductive system is impaired to such an extent that resin flow is interrupted and the tree is unable to resist a beetle attack.

Salman and Johnson (*U288*) studied the relation of tree susceptibility to the healed-over scars of mines made by flatheaded borer larvae in the cambium area. It was demonstrated by a special technique using silver nitrate that these scars have a definite blocking effect upon the movement of liquids through adjacent wood layers, and thus are detrimental to normal conduction. The high incidence of flatheaded borer infections in high-risk trees of eastside pine types shows that such infections are undoubtedly a factor in the general susceptibility complex. On the other hand, indications that successful incipient infestations of the flatheaded borer often occur in slow-growing trees may show that the conductive function has been declining at the time of attack.

Transpiration

Studies of tree susceptibility have not included any attempt to distinguish between the functions of conduction and transpiration. These two functions are so closely linked that failure of one will inevitably result in impairment of the other. Although no formal reports dealing with transpiration are available, some attention has been given to the effects that follow complete defoliation of a tree. When trees are defoliated by insects or fire, the result is an accumulation of excess moisture in the inner bark and sapwood which is unfavorable to the development of western pine beetle broods.

Phloem Moisture

Beal (*U3*) made a study in the Klamath Basin of eastern Oregon in 1929 to determine the role of moisture in the phloem tissues of the tree as a contributing factor to susceptibility. He approached the problem by using as a basis the known degree of susceptibility of Keen's different tree classes. Phloem samples were collected from representative trees in each class and 5 duplicating samples were taken from each crown class in each age group—80 samples in all. Phloem moisture was determined on a dry weight basis. From the correlations obtained by plotting phloem moisture content against the susceptibility rating in each class, Beal concluded that:

> There exists a very close correlation between the phloem moisture content of western yellow pines and their susceptibility to attack by the western pine beetle. Generally speaking the moisture of the phloem decreases with the size of the crown, there being little difference in the age classes. The beetle loss increases as the moisture decreases until a point is reached which appears to be too dry to attract the beetles. This condition is to be found with the (D) crowns.

Hall (*U88*) made a similar study in August 1948 at Blacks Mountain Experimental Forest in California by sampling the phloem

moisture of 4 trees in each of Keen's 16 tree classes, also sampling the 4 risk groups. This test failed to show any consistent association between phloem moisture and either tree class or risk class.[4]

Differences of phloem thickness showed a broad association with both tree class and risk group. The average phloem thicknesses by class were Class A trees—0.30 inches; Class B—0.24 inches; Class C—0.16 inches; and Class D—0.13 inches. The average phloem thicknesses by risk were Risk I—0.27 inches; Risk II—0.20 inches; Risk III—0.16 inches; and Risk IV—0.13 inches.

Condition of the Root System

The root system of a tree is of major importance to the tree's growth, vigor, and resistance to attack by the western pine beetle. In spite of the difficulties and cost of examining root systems, forest entomologists have conducted a few studies in this field.

In 1926, Person (*U238*) partially pruned the roots of two fast-growing ponderosa pines in an attempt to determine whether the reduction of the root area would cause the trees to attract the western pine beetle. Although these root-pruned trees did attract some red turpentine beetle attacks, Person considered the results as negative and concluded: "Root-pruned trees are evidently not attractive (to the western pine beetle), at least during the first season following treatment." Since this experiment was concerned with artificial injury to the roots of normally vigorous trees, it did not reveal much about the natural deterioration of the root system in high-risk trees.

West (*U330*) examined the exposed root systems of five ponderosa pines upturned by a windstorm in the eastside pine type of Modoc National Forest, Calif. These windfalls included one low-risk and four high-risk trees. He found that the low-risk tree and three of the high-risk trees had extensive and apparently healthy root systems, but the fourth high-risk tree had a root system that was much reduced and abnormal.

During the early summer of 1940, Johnson (*U112*) examined parts of the root systems of six ponderosa pines in the same eastside pine type. With CCC workers using picks and shovels to remove soil, he studied the roots of five low-risk and one high-risk trees. The crowns of these trees were also carefully studied and an inventory taken of the *Matsucoccus* scale population on limbs and twigs and of the incipient flathead infestation on the main bole. Johnson reported that "the root system of the Risk IV tree showed many more dead large roots and branches, and was considered to be in poorer condition than the root systems of the Risk I trees."

In 1941 Bedard (*U13*, *U14*) used hydraulic pressure to wash out the root systems of six ponderosa pines of known risk ratings in the Klamath Basin near Bly, Oreg. He summarized previous studies on ponderosa pine root systems and reviewed literature pertaining

[4] The difference in results between Hall's and Beal's studies may be due to differences in soil moisture in the years in which the studies were conducted. The year 1929 was a drought year, while 1948 was a year of above-normal precipitation.

to root anatomy, morphology, and physiology. In connection with this review, he stated:

> Root form is quite specific, and in addition there is considerable reciprocity between the crown and root system. Root development is of critical importance to continued plant growth. It is important that root development keep pace with crown development.

In the Klamath Basin study, Bedard selected three pairs of high-risk and low-risk mature ponderosa pines on a site where it was practical to wash out the root system. The results did little more than reveal some physical differences between high- and low-risk trees.

> In the low risk trees, the roots branch from the main axis deeper below the soil surface and penetrate the soil at a greater angle than the roots of high-risk trees. Additional slight differences were found but they were not statistically significant. These differences were that high risk trees had fewer roots of smaller size, a greater percentage of dead roots, and fewer small feeding roots per lineal foot.

In summing up these studies, Bedard listed the following factors as essential to root development: Physical and chemical properties of the soil, soil moisture, mycorrhizae, soil gases, heat, toxic decomposition residues, competition, beneficial plant associates, and heredity. A further study of root conditions using very small trees and potted seedlings and a series of soil treatments was reported in 1944 (*U21*).

None of the root studies to date has shown any significant relation between condition of the mycorrhiza on the roots and the susceptibility of ponderosa pines. Difficulties in the way of thorough examinations of the root systems of any number of trees have apparently discouraged even preliminary explorations in this field.

Pathological Factors

Fungi, disease, and other pathological agents that affect trees can in many cases increase the trees' susceptibility to insect attack. Frequently insects are the vectors of plant diseases, or there may be a symbiotic relation between the disease and the insect. Some study has been given to the pathological factors that affect ponderosa pine and to their relation to this tree's susceptibility to western pine beetle attack.

Needle Fungi

Elytroderma deformans is a serious needle disease of ponderosa pine throughout the tree's range in the West. It also attacks Jeffrey, lodgepole, and pinyon pine in the Western States, and several species of pine in the East. Severe damage, however, has been reported only on ponderosa and Jeffrey pine in California, Oregon, Washington, and Idaho. Recently it has become exceedingly destructive to ponderosa pine stands in central Oregon and southern Idaho. These outbreaks have been under study, and the most recent information has been published (*84*).

The fungus has a life cycle of one year. It attacks needles of the current year's growth during the latter part of the growing season.

By the next May and June, the needles turn a reddish color for most of their length while the base remains green, or the entire needle may discolor. Apparently the fungus produces some toxin which is carried down into the stems and causes internal lesions of the twigs. Repeated attacks cause dwarfing of the twigs, the formation of loose witches' brooms, or death of the twigs and branches. Trees heavily affected year after year become weakened and ultimately succumb to the disease or to the attack by bark beetles.

While the disease has been known since 1913 and has appeared periodically in spot infections, it was not until about 1945 that its potential destructiveness was fully appreciated. It became epidemic and killed out nearly the entire ponderosa pine stand on the Johnson Creek area of Ochoco National Forest in Oregon. Since 1945 it has persisted in epidemic form in a number of areas in eastern Oregon and on Boise and Payette National Forests of southern Idaho. The disease seems to favor cool ravines or basins, particularly at higher elevations where pine is associated with fir, lodgepole, or larch.

The effect of this needle disease in weakening pines and causing them to become more susceptible to bark beetles has been of great concern to foresters and forest entomologists. The Johnson Creek infection in Oregon developed so rapidly and with such virulence that trees were quickly defoliated and killed. The phloem and sapwood of these defoliated trees developed excessive moisture or a "sour sap" condition. This apparently made them unattractive to the western pine beetle, since no bark beetle outbreak developed in these disease-stricken areas.

In southern Idaho forests, however, the disease progressed more slowly. Trees were repeatedly attacked, progressively lost foliage, developed twig lesions, and decreased in growth rate. This decline in tree vigor increased the susceptibility to bark beetles. As a consequence, there was a general increase in beetle activity in the disease-infected areas. On the Deadwood Reservoir area of Boise National Forest, a western pine beetle outbreak developed such intensity in the needle-disease-weakened timber that a beetle control project was started. In 1951, 2,200 trees were treated; in 1952, 900 were treated, and the infestation was reduced to 200 trees. The area was logged in 1953.

On the Warm Lake area of Payette National Forest and on other areas in southern Idaho and eastern Oregon, deterioration of the trees' crown vigor caused by progressive infections of this needle disease has created a serious problem of risk rating and marking for selective cutting. Due to progress of the disease, some areas have had to be remarked and relogged several times; the infected areas were practically clear cut.

The *Lophodermium* fungi associated with the early shedding of older needle fascicles may at times produce an appearance of color in pine foliage. When the attacked needles drop, the tree appears to have a thin-crown for a season or two until it builds back its normal needle complement. However, no studies have been made to determine what effect fungi have upon permanent deterioration of the crown. Apparently they do nothing more than accelerate at times the normal shedding of older needles. The earlier opinion of

the pathogenicity of *Lophodermium* has been discounted by later studies, and Dr. Willis Wagener in a note on the subject states: "It seems safe to say that the fungus has no appreciable effect on the growth of ponderosa pines or on their risk rating."

A needle-cast fungus, identified by Dr. Wagener as *Hypodermella medusa*, caused some confusion in rating the risk of a few individual trees on Blacks Mountain Experimental Forest during 1940. This fungus usually attacks only needles that are 2 years or more old. In 1940 it attacked a few trees that had previously been rated as low risk. Because they shed practically all needle except those of the 1939 and 1940 growth, these trees were later given a more severe appraisal of risk. This situation was complicated by a drought that caused shortened needle growth in 1939. The condition was only temporary, and normal needle growth was restored in subsequent years.

Later examinations by Dr. Wagener at about 2-year intervals from 1940 to 1951 showed that the same trees were always affected with the disease. The 1940 infection, however, was heavier than that in any of the subsequent years.

Root Fungi

A root disease of young Jeffrey pines, first noted by K. A. Salman in 1934 on Lassen National Forest in northeastern California, was studied by Olson (*102*), who named it as a new species. In 1941 Dr. Donald DeLeon found a root disease contributing to the death of many Jeffrey pines on the Mount Laguna Recreational Area of Cleveland National Forest in southern California. This disease was studied by Dr. Willis Wagener who determined it to be *Fomes annosus*. Later it was shown that this was the same disease described by Olson. Dr. Wagener made a series of field studies to determine the prevalence and distribution of this fungus on the root systems of ponderosa and Jeffrey pines. In a letter to the Regional Forester dated October 16, 1946, he reported as follows:

> Within the past few weeks explorations around the bases of distressed, dying, or recently dead trees in parts of northern California have shown that root killing of large pines by *Fomes annosus* is not confined to southern California, but occurs in at least some portions of northern California as well. Part of the field examinations were made jointly with Dr. Donald DeLeon of the Berkeley Laboratory and part by our office alone. The disease has been found in portions of the eastern Plumas, Lassen, and Shasta National Forests, including the Blacks Mountain Experimental Forest, and in Lassen Volcanic National Park. In addition to ponderosa and Jeffrey pines, sugar pine has been found to be affected and there is some indication that white and red firs are subject to attack.

Additional studies by Wagener and Cave uncovered much new information concerning the behavior of this disease and its relation to bark beetle attack. In their published article (*137*) they state:

> Killing of the bark and cambium of attacked trees by the fungus (*Fomes annosus*) ordinarily extends little above the ground level. Except in quite small trees, the balance of the trunk usually is invaded by bark or wood-boring beetles before fading

of the foliage occurs as a result of girdling from the fungus attack, and thereafter the tree appears superficially no different from one killed primarily by bark beetles.

Bark killed by the fungus separates readily from the wood. The separated surfaces are usually a characteristic light brownish buff in color, finely penciled with light russet, or the reverse. . . . A thin weft of whitish mycelium is also usually visible between wood and bark. . . . Another confirmatory feature in the cambial region and in bark killed by the fungus is the absence of galleries of the red turpentine beetle (*Dendroctonus valens* Lec.). This beetle and its larvae are usually active in the basal portion of pines killed primarily by insects but apparently avoid bark invaded by *Fomes annosus*. . . . The wood around the site of initial infection, usually on a root, becomes heavily infiltrated with resin. . . . After a tree is killed the fungus remains active as a wood-rotting organism in the roots and butt.

The disease spreads from an initial center, usually a stump or snag, to surrounding trees through contact of overlapping root systems, forming a roughly circular opening in stands on level ground.

In addition to the direct threat to surrounding trees offered by the fungus, an accompanying danger has been observed in one or two localities near the lower ecological limits for pine. Here bark beetles, presumably species of *Ips*, have developed in trees killed primarily by the fungus and, on emergence, have extended their attack to adjoining trees showing no evidence of the disease at the base. In other infected districts less marginal for pine no similar extension of bark beetle attacks from diseased trees has been noted, but it is quite possible that such trees may contribute to the building up of bark beetle epidemics by providing a favorable environment for the maintenance of a small beetle population during periods when infestation is in an endemic status.[5]

Another root disease, reported by Bongberg in 1939 on Blacks Mountain Experimental Forest, was identified by Wagener as a species of *Leptographium*. The tree apparently had been killed by this fungus, which originated in the roots and invaded the main bole above the root collar. The fungus caused a brown stain in the sapwood. The only insects found in this tree were the pine flatheaded borer and adults of a sour-sap beetle (*Hylurgops subcostulatus* (Mann.)) near the base. Both of these beetles were considered to be secondary.

The shoestring root rot *Armillaria mellea* has been observed killing ponderosa pines of small diameter, usually trees of poor vigor in intermediate or suppressed positions. These trees are usually attacked in the main bole by the mountain pine beetle, emarginate ips, or by species of flatheaded borers. The infrequency of trees killed by this fungus indicates that it is not an important primary root disease in ponderosa pine stands.

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[5] Reviewing the above paragraph, Dr. Wagener commented in 1954: "At the time this article was written, we were not aware of the fairly long-period rise and decline in incidence which evidently is tied in with soil moisture in some way, though we are not certain what the particular conditions are that favor the disease. For the last few years it has been at a rather low ebb in most of California."

Heart Rots

Observations indicate that there may be some degree of correlation between heart rots in ponderosa pine and high risk to bark beetle attack. Heart rots are common in old trees of poor thrift, in spike-top trees, and in those with broken tops and limbs. Since these decadent trees are often of high risk, it is understandable why there should be some degree of positive correlation with heart rots. Also, it may be that heart rots actually cause a decline in tree vigor and thus contribute to susceptibility. This relationship in ponderosa pine has not been given careful study (*138*).

Dwarfmistletoe

As early as 1916, it was suggested that dwarfmistletoe (*Arceuthobium campylopodum* forma *typicum* (Engelm.) Gill) and the witches'-brooms it causes may increase susceptibility of ponderosa pines to attack by the western pine beetle and thus serve as focal points for infestations (*145*). Observations have been made on this point for many years without conclusive evidence to show a direct relationship.

During the field seasons of 1914, 1915, and 1916, Burke (*15*) spent part of his time on a project entitled "The relation of mistletoe on living trees to attacks by tree-killing insects." He found "that 64 percent of virgin growth yellow pine . . . in typical areas near Pyramid Ranger Station above Placerville, California, were mistletoe-infected. The conclusions drawn from the study were: (a) trees infected by mistletoe are not more subject to attack by *Dendroctonus* beetles than trees not so infected; in fact, it looked as though badly infected trees were less liable to attack than trees free of infection; and (b) trees weakened by mistletoe do not contribute to the increase of *Dendroctonus* beetles."

Of 372 trees killed by the western pine beetle on the Lamb's Mine Unit at Ashland, Oreg., Keen (*U127*) found that 38 percent were infected with mistletoe and 57 percent had advanced cases of witches'-brooms. He did not determine what percent of the green stand was similarly affected.

Hopping (*52*) summarized the information on the occurrence of mistletoe infection on 1,656 beetle-killed trees treated on the Susan River Control Project, Lassen National Forest, Calif. This record showed that mistletoe was present on 15 to 26 percent of the infested trees. But since Hopping also failed to determine what percent of mistletoe-infected trees occurred in the green stand, the degree of selection was not shown.

In a series of 6,535 tagged trees on thirty 10-acre plots in eastern Oregon, a total of 286 trees were killed by beetles in 10 years. These trees were rated as follows:

Tree condition:	*Number killed*	*Total trees*	*Percent killed*	*Mortality ratio*
No mistletoe noted	249	6,218	4.0	0.9
Small amount of mistletoe	0	25	0	0
Large amount of mistletoe	3	19	15.8	3.6
Small witches' brooms	12	171	7.0	1.6
Large witches' brooms	22	102	21.6	5.0
Total or average	286	6,535	4.37	1.0

These Oregon plot data confirm the early suspicion that mistletoe-infected trees are more susceptible to beetle attack than normal trees. Trees with large amounts of mistletoe are 3.6 times as susceptible, while those with large witches'-brooms are 5 times more susceptible. This gross relationship does not take into account that trees heavily infected with mistletoe are probably also the older, more decadent tree classes in a stand. The fact that so many trees without mistletoe infection are killed by beetles probably was the reason for Burke's (*15*) conclusion that trees affected by mistletoe do not contribute importantly to western pine beetle infestations.

Insect Injuries

The extent to which other insects may contribute to the weakening and increased susceptibility of ponderosa pine has been discussed in Section II, p. 102.

Mechanical Injuries

Trees injured by lightning, fires, top-killing insects, girdling, or mechanical bark injuries, are frequently attacked by the western pine beetle. The degree of susceptibility developed by such injuries has been the subject of numerous studies.

Lightning-Struck Trees

Lightning injury was one of the first factors considered to be a cause of the attraction of bark beetles to pine trees. Hopkins (*44*) states that:

> In certain sections of the country where a great many pine and spruce trees are struck by lightning during the summer months these trees furnish exceptionally favorable conditions for the perpetuation and multiplication of the pine and spruce beetles. . . . This is especially true in the Southern States where a pine tree struck by lightning attracts the beetles to the spot, and they not only enter the injured tree but attack and kill a number of those surrounding it.

In ponderosa pine stands, lightning-struck trees have always been regarded as especially attractive to the western pine beetle. Hopping (*52*) states:

> If there is an epidemic infestation within the area every lightning-struck tree becomes infested. If, however, the infestation is very light on an area, lightning-struck trees often escape being attacked.

Keen (*62*) makes this generalization:

> Lightning-struck trees appear to be very attractive to bark-beetles, and very few escape death if beetles are present in any numbers. In fact, unless lightning-struck trees are completely shattered, they rarely die unless attacked by the insects.

Yet no studies on record show the degree of preference or the percentage of lightning-struck trees that are attacked by beetles. Since it has not been shown that longitudinal lightning scars down the main trunk affect growth rate to any extent, there is no explana-

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tion for beetle attraction unless it is due to changes that take place in the sapwood and phloem tissues as a result of the electrical charge breaking down cells.

Fire Scars

Basal scars or "cat-faces" made by fire also result in exposure and overheating of the cambium and sapwood. Results from studies of the Northfork Burn by Miller (*U199*) and of the Sugar Hill fire by Salman and Wohletz (*U290*) indicate that the common basal fire scars in pine stands, and the subsequent extension of such scars by repeated fires, has no effect upon the susceptibility of the trees to bark beetle attack. On the other hand, Bedard (*U12*) analyzed the characters associated with high risk and found that "fire scars were more abundant on high-risk trees than on normal trees." He suggested that they should "not be overlooked as a possible clue to the cause of (some) tree decline."

On risk plots in eastern Oregon, Keen (*U166*) found that trees with small fire scars (less than 50 percent of the basal circumference) were not particularly susceptible. But out of 233 trees with large basal fire scars, 7.3 percent were killed by beetles in 10 years. Since the average kill in the stand was 4.37 percent, these large fire-scarred trees showed a mortality ratio of 1.7. In other words, they were nearly one and three quarter times as susceptible as the average trees.

Top-Killing

Keen (*U127*) found on the Ashland, Oreg., areas that trees top-killed by *Ips* were definitely more attractive to the western pine beetle than uninjured trees; over 26 percent of such trees were attacked in one season. On the Cascadel area of Sierra National Forest, Calif., Person (*U238*) found that 43 percent of trees top-killed by the California five-spined engraver were attacked by the western pine beetle within 2 years after top-killing.

Hall (*U78*) reported that old top-kills were an important factor in the seasonal loss on Modoc National Forest in California:

> Of the total volume loss for 1938, previously top-killed trees made up 36 percent of the volume. However, the indirect effect of top-kills in the 1938 loss appears to be of additional importance, because in a large percent of cases, old top-killed trees served as a focal point of infestation in a group, where the insects first attacked the top-kill and then overflowed into adjacent vigorous trees.

Johnson (*U114*) analyzed the distribution of top-killed trees in the 1940 loss on Blacks Mountain Experimental Forest. Of 621 beetle-killed trees found that year, 33 percent of the trees and 38 percent of the volume had been previously top-killed. In the green stand as a whole, only 6.7 percent of the trees and 9 percent of the volume was in the top-killed category. Johnson concluded that:

> Top-killed trees show a death rate almost five times the expectancy based upon their occurrence in the green stand. This mortality rate is seven times that of trees without top-kills.

All top-killed trees except the young dominants appear to be markedly susceptible to insect attack. Top-killed trees of mature and overmature age appear to be particularly susceptible to insect attack.

On study plots in Oregon, Keen (*U166*) found that the relative susceptibility of active spike tops (those with some current infestation as shown by fading or red needles), old spike tops, and broken-top trees was affected as follows:

Tree condition:	*Trees killed*	*Total trees*	*Percent killed*	*Mortality ratio*
Normal top trees	215	6, 004	3. 6	0. 8
Active spike tops	29	85	34. 1	7. 8
Old spikes	37	408	9. 1	2. 1
Broken tops	5	38	13. 2	3. 0
Total or average	286	6, 535	4. 4	1. 0

This record shows that active spike tops are very susceptible to attack by the western pine beetle, and are killed nearly eight times as frequently as average trees. Old spikes are taken twice as often, broken tops three times as often.

Freezing

Salman (*U275*) observed that low winter temperatures of January 1937 on Modoc National Forest, Calif., scorched foliage at the tops of trees and injured the phloem of some trees to such an extent that the trees were attacked and killed by secondary bark borers. In trees injured by the cold, the roundheaded borers *Acanthocinus spectabilis* Lec. and *A. obliquus* Lec. were, in many cases, the first species to enter the cambium area and were successful in rearing broods. Assisted by the engraver beetles *Orthotomicus ornatus* and *Ips oregoni*, they successfully competed with the flatheaded borer *Melanophila gentilis*. The base of these cold-injured trees filled in with the red turpentine beetle, and in some cases this beetle took precedence in its attack over all other species.

Freezing injury to tops of trees has been reported by Wagener (*136*) and may precede attacks by engraver and twig beetles, and other primary or secondary bark beetles and borers. This type of injury may be more common than has been recognized, and may be the primary cause of top-killing which has frequently been ascribed to bark beetles.

Other Types of Injury

Other types of injury and special conditions that make trees attractive to the western pine beetle are described under "Results of Attraction Studies" in Section I, p. 40.

Silvical Factors

Although the slowing down of a tree's growth is a dominant factor in attracting beetles or making the tree susceptible to their attack, many slow-growing trees have survived for years without being subjected to attack. In addition to rate of growth, the silvical factors of tree age, size, degree of maturity, crown size, position

or degree of dominance, and general tree vigor and health were early recognized as having a possible connection with tree resistance and susceptibility.

Hopkins (*44*) noted that the western pine beetle preferred to attack "weakened and felled trees" and "large mature timber" while areas of "vigorous, recently mature, or young growth" were unfavorable for attack. He did not imply that growth rate was an important element of tree resistance and susceptibility. As a matter of fact, he repeatedly pointed out that this beetle attacked healthy trees.

Keen (*U127*) analyzed the type of tree attacked by the western pine beetle during the years 1914–16 on the Lamb's Mine Unit near Ashland, Oreg. Of the total of 401 trees that were killed, 45.4 percent were "thrifty," 35.9 percent were "mature," 11.5 percent were "decadent," and 7.2 percent were "felled." The thrifty trees were "young, before maturity of growth"; mature trees were "those that have reached the maximum growth and have developed flat crowns"; decadent trees were "old, not vigorous, and in a retarded state of growth"; while felled trees were those that had been blown or knocked down by wind or other causes. No comparison was made between these percentages and the distribution of these classes in the stand as a whole.

Tree Age or Maturity

Hopkins (*44*) stated:

> Practically all of the more destructive species (*Dendroctonus*) show a decided preference for the larger and best-matured trees, and as a rule these are killed first, and the younger timber is not attacked until later, if at all. This is particularly true of . . . the western pine beetle, and the mountain pine beetle of the West.

While the impression still persists that overmaturity is the most important factor in susceptibility, later studies have shown that it is of less importance than tree health and vigor.

Keen (*U151*) compared the age groups of 27,465 ponderosa pines, beetle-killed during the highly epidemic 4-year period 1928–31, with age distribution of 22,428 green trees on 16,000 acres of sample plots in southern Oregon and northern California. He found the following ratio of mortality by age groups:

Age group:	*Tree age (years)*	*Total stand (percent)*	*Beetle-killed (percent)*	*Ratio of mortality to stand*
1	--75	17. 6	8. 3	0. 46
2	75–150	25. 8	28. 2	1. 15
3	150–300	29. 6	32. 3	1. 05
4	+300	27. 0	31. 2	1. 16

Regarding this tabulation, Keen noted:

> There is very little difference in relative susceptibility by ages in trees over 75 years of age. As has been frequently noted, trees of the bull pine type (age group 1) which rarely exceed 16 inches in diameter in Oregon's site 4, are very resistant to bark beetle attack.

Additional evidence accumulated from surveys in eastern Oregon, Washington, and northern California during the endemic period between 1938 and 1940 with a total sample of 51,409 beetle-killed trees (*71*) gave the following results:

Age group:	*Tree age (years)*	*Total stand (percent)*	*Beetle-killed (percent)*	*Ratio of mortality to stand*
1	−75	17. 7	5. 8	0. 33
2	75–150	25. 4	21. 4	. 84
3	150–300	42. 4	42. 8	1. 01
4	+300	14. 5	30. 0	2. 07

This evidence indicates a marked increase of susceptibility in overmature trees and a strong resistance of young and immature groups, particularly during endemic conditions.

Between 1936 and 1940, Bongberg (*U30*) compared the occurrence of insect-caused loss in 404 ponderosa pines on Blacks Mountain Experimental Forest with age distribution within the green stand. He found the highest percentage of volume loss in the overmature age class. He states: "It is evident that risk does increase with age, but age does not become an important factor until overmaturity is reached . . . Age does not overshadow or outweigh the importance of risk characters as an indicator of susceptibility." This appears to sum up the conclusions reached on the importance of age in the studies conducted so far.

Tree Size

One of the first selective tendencies recognized by observers was that trees in the middle range of diameters were killed by the western pine beetle more frequently than smaller or larger trees. This preference was demonstrated by comparing the curve of diameter distribution for beetle-killed trees with a similar curve for the entire stand. Such a comparison by Person (*111. U238*) used the records from 5,000 beetle-killed trees on the San Joaquin Control Project and the diameter distribution of ponderosa pine in the stand as determined by Burnett Sanford of the U. S. Forest Service. These data, all from westside Sierra pine type, showed that:

> The number of trees killed in the diameter classes between 20 and 30 inches is much greater than proportionate to the number of such trees in the total stand. Evidently the western pine beetle prefers trees between 20 and 30 inches in diameter.

Keen (*U151*) used data from 6 years of sample-plot cruising in southern Oregon and northern California (1927 through 1932) to compare the frequency distribution by 2-inch diameter classes of 49,701 beetle-killed trees with 64,159 green trees (fig. 39). This comparison showed a marked preference by the beetles for trees between 20 and 32 inches d.b.h., a confirmation of earlier work.

Since beetles lack the faculty needed to distinguish trees by diameter measurements, why should they select trees within these particular diameter limits? The evidence suggests this reason: The greatest struggle of mature trees for dominance occurs in this diameter range. Many young trees, up to 20 inches d.b.h., are

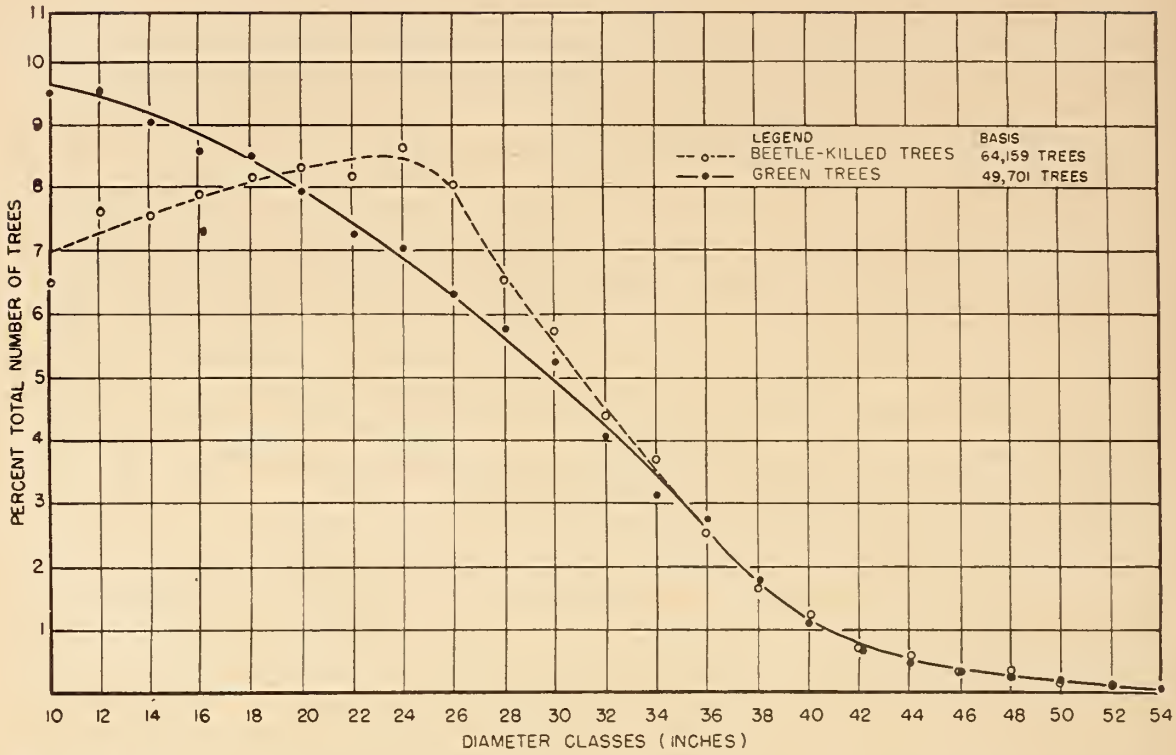

FIGURE 39.—Distribution of green and beetle-killed trees by diameter classes, eastside type. Southern Oregon-northern California, 1927–32.

eliminated from the stand because of suppression before they have reached a size with bark characters to make them attractive to the western pine beetle. Then, as maturity approaches, the competitive struggle for dominance becomes intense and many stems are eliminated. After the trees reach 32 inches d.b.h., most of the trees in the stand are mature and overmature dominants and codominants that have survived the struggle and are well fitted to maintain their positions unchallenged.

Crown Size, Position, or Dominance

In studies of tree selection by the western pine beetle, Person (*U237*) considered crown characteristics in relation to susceptibility. About 200 ponderosa pines killed by the western pine beetle were marked on the Cascadel area in 1925 and classified as to dominance, crown shape, length, and width. Since he did not have a similar comparison for the green trees in the stand, Person could not draw conclusions as to degree of selectivity. He stated, however:

> It is evident that the average tree of dominant and codominant crown class with rounded top and medium length and width of crown suffers the heaviest loss. It is surprising that the number of intermediate and suppressed trees killed is so small. This is probably due to the fact that the total number of such trees in the stand is small because of the openness of the stand.

In a later report on his Cascadel studies, Person (*U242*) stated his conclusion as to the relation of crown form to susceptibility as follows:

> The susceptibility of a tree varies inversely with the size of its crown. Trees with long, wide crowns are least susceptible to

attack by the western pine beetle and trees with short, narrow crowns are most susceptible.

When Dunning (*31*) developed his "Tree Classification for the Selection Forests of the Sierra Nevada," he pointed out that "the small-crowned mature codominants of class 4 are indicated to be the most liable to insect damage."

In his study of relative susceptibility of ponderosa pine to bark beetle attack, Keen (*U151*) compared the frequency of attack in four crown vigor groups. To a large extent, these groups represented four degrees of thrift, crown size, and dominance. Comparing 49,701 beetle-killed trees with 64,159 green trees on sample plots in southern Oregon gave the following results:

Crown vigor group:	*Total stand (percent)*	*Beetle-killed (percent)*	*Ratio of mortality to stand*
A—Full vigor	36. 0	12. 0	0. 33
B—Moderate vigor	36. 0	35. 3	. 98
C—Poor vigor	21. 2	43. 4	2. 05
D—Very poor vigor	6. 8	9. 3	1. 37

Keen states:

> It is evident from these comparisons that crown vigor is much more important in determining susceptibility than merely age. In other words, the fact that a tree is old does not necessarily make it a poor risk, while the character of its crown and its position in the stand are much more important considerations.

Crown Vigor and Health

Crown vigor or thrift was also recognized by Hopkins (*44*) as an important factor in the selection of trees by the western pine beetle. He states ". . . it appears that this species prefers to attack weakened and felled trees, or isolated healthy ones." The attraction studies started in 1916 also indicated this beetle's preference for felled trees, top-killed trees, and those of slow growth. Many other studies have followed, all of which were directed toward finding symptoms of poor health, weakness, or injury that would give a clue to susceptibility. Most of this work was done in connection with the development of tree classifications.

Key Trees in Groups

Under epidemic conditions, the western pine beetle attacks groups of trees without regard to tree position, crown class, size, age, or growth vigor. However, in each group there is usually a tree to which the beetles are first attracted and on which they concentrate during the first phase of the attack. This initial "key" tree as a rule exhibits one or several of the symptoms of susceptibility, such as suppressed growth, deteriorated crown, or some special injury to the trunk, crown, or roots. Once the beetles have occupied the bark area of this "key tree," more beetles coming to the vicinity attack adjacent trees, regardless of their condition, until the beetle population coming to that particular center of attraction has been absorbed.

These "key trees" are undoubtedly quite important to the ecology of the western pine beetle. Under endemic conditions most of the trees attacked are "key trees." In this way the western pine beetle is able to perpetuate its population by breeding in weakened trees when the general stand conditions are unfavorable to an increase of its numbers.

Tree Classifications

Classification of trees according to age and crown vigor has been a further step in the recognition of susceptible trees. At least three such classification systems have been developed, all having silvicultural as well as entomological uses. Based on visual characters that can be readily seen and appraised in the woods, the systems apply to ponderosa pine stands where western pine beetle infestations are prevalent.

Dunning Tree Classes

Dunning (*31*) was the first to develop a tree classification for ponderosa pines in uneven-aged forests of the Sierra Nevada. He defined seven classes of trees that could be distinguished by age characters, tree position, and form of the crown. The classes were intended as a measure of tree vigor to serve silvicultural purposes, such as the selection of trees for cutting or for reserve on timber sales. The fact that trees with least vigor—represented by Dunning's Classes 7, 4, and 5—were those with the highest rates of mortality from beetle attack opened an entomological application for this classification.

During the 1927 survey of 19,680 acres of sample plots in eastern Oregon, 13,160 beetle-killed trees were classified according to Dunning's tree classes. In addition these tree classes were applied to a sample of 10,053 green trees. Keen (*U144*) compared the distribution of the killed trees to that of the green trees in the stand, and the results confirmed Dunning's findings. Beetles showed the greatest preference for Classes 4, 5, and 7, all of which were making annual growth of less than 1 percent of basal area per year. Keen also concluded from this study that:

> Eighty percent of the loss by volume consists of the overmature dominant trees of Class 5 . . . In dominant classes, the average volume of trees killed by beetles is much lower than the average volume of the class as a whole . . . On good sites there is a marked selection of the suppressed and codominant trees of Classes 4 and 7. As the site becomes poorer the proportion of loss increases in the dominant classes 1, 3, and 5 and decreases in the codominant, intermediate, and suppressed classes 2, 4, 6, and 7.
>
> The results of this study emphasize the importance of marking for removal trees of classes 4, 5, and 7. It also indicates that perhaps more smaller-diameter trees in classes 4, 5, and 7 should be removed than has heretofore been the practice. Class 3 trees are the safest risk where large trees are needed for seed or where reserve volume of valuable material is desired. Class 2 trees are a relatively poor risk and should be removed in preference to Class 1 trees where groups are to be thinned.

The selective thinning of stands with the removal of susceptible trees offers hope of greatly reducing the loss from insects, especially on the better sites.

This study also indicated a wide dispersion of mortality rates within certain tree classes and suggested that further subdivision of these classes might be helpful in segregating the more susceptible types.

Keen Tree Classes

In the hope of obtaining a more precise grouping of trees showing similar mortality rates or degrees of bark beetle susceptibility, Keen expanded Dunning's classification by using the basic conceptions of age, crown size, and dominance. Trees were divided into four primary age groups: Class 1, young; Class 2, immature; Class 3, mature; and Class 4, overmature; and into four crown-vigor groups: A—full, long, dominant crowns; B—full, shorter, codominant crowns; C—narrow, long, intermediate crowns; and D—short, narrow, suppressed crowns. The combination of 4 ages and 4 crown-vigor groups made a total of 16 classes possible (fig. 40, tables 3 and 4).

Analysis of 27,465 beetle-killed trees occurring on 15,000 acres of sample plots in northeastern California and eastern Oregon between 1928 and 1931 showed that the highest proportion of losses was occurring in trees of poorest vigor, i.e. those of C and D crowns, and to a less marked degree in those of the older age Classes 3 and 4. The first results of this study were published by Keen (*68*). In a later article (*71*), the characters separating the different classes were redefined and clarified after a detailed study of sample plots had indicated the characters most important in grouping trees of similar growth rates.

An analysis of survey data from 112,409 acres of sample plots in eastern Oregon during the period 1928–40 (*71*), wherein 51,409 trees killed by the western pine beetle were compared with a sample of 206,037 green trees, showed the overage mortality ratio [6] of trees killed in the different classes to be as follows:

Keen's age class:	*Keen's vigor class*				*Average by age*
	A	*B*	*C*	*D*	
1	0. 1	0. 3	0. 8	1. 1	0. 3
2	. 2	. 6	1. 0	1. 5	. 8
3	. 3	1. 0	1. 9	2. 6	1. 0
4	. 4	1. 4	2. 7	3. 8	2. 1
Average	. 3	. 7	1. 8	1. 7	1. 0

In connection with an intensive study of the tree characters most valuable in judging risk of ponderosa pine to western pine beetle attack (*U166*), increment cores were taken in 1938 and 1939 from almost 8,000 trees, representing all of Keen's tree classes on a series of thirty 10-acre tagged tree plots in eastern Oregon. These cores were later measured by workers of the Forest Insect Laboratory at

[6] A measure of relative risk obtained by dividing the percent of occurrence of mortality in a given class by the percent occurrence of total trees, living and dead, in this class.

FIGURE 40.—A ponderosa pine tree classification based on age and vigor.

TABLE 3.—*Description of Keen's age classes*

Character	Class 1	Class 2	Class 3	Class 4
Maturity	Young	Immature	Mature	Overmature.
Age	Usually less than 80 years	Approximately 80 to 180 years	Approximately 180 to 300 years	More than 300 years.
Diameter breast high	Rarely over 20 inches	Rarely over 30 inches	Rarely over 40 inches	Usually large diameters in dominant trees.
Height	In lower canopy usually less than 60% of total height of mature canopy.	Height usually less than 90% of total height of mature canopy.	Height practically that of general crown canopy (except of intermediate, suppressed, or top-killed trees).	Full height of general canopy (except suppressed, spike-topped or broken trees).
Growth and taper	Thrifty trees making rapid height and diameter growth; rapid taper.	Considerable height growth still in progress; good diameter growth in thrifty trees; taper considerable.	Height growth practically complete; diameter growth slow; moderate taper.	Making no height growth; diameter growth very slow; least taper.
Bark color	Dark grayish brown to black (except at extreme base).	Dark reddish brown on lower half of bole; dark bark on upper half.	Light reddish brown on lower three-fourths of bole; dark bark showing in upper one-fourth of bole.	Light yellow; uniform color throughout bole (except at extreme top).
Bark plates	No plates; rough bark, deeply furrowed, with narrow ridges between fissures.	Narrow smooth plates between fissures.	Moderately large plates between fissures.	Plates usually very wide, long, and smooth; fissures often rather shallow.
Branches	Branches upturned in upper three-fourths of crown; small for diameter of bole.	Mostly upturned in upper half of crown; lower half horizontal or drooping; small to medium for diameter of bole.	Upturned near top; middle horizontal; lower ones drooping; moderate for size of bole.	Large, heavy limbs, often gnarled or crooked; mostly drooping, except in extreme top.
Whorls	Whorls distinct in upper crown	Whorls distinct in upper half of crown.	Whorls indistinct except at extreme top of crown.	Whorls indistinct and incomplete.
Top	Top usually pointed	Top usually pointed, sometimes rounded.	Top usually pyramidal or rounded, sometimes pointed.	Usually flat, occasionally rounded or irregular.

NOTE: Description primarily applicable to central and southern Oregon and northern California, Site IV.

TABLE 4.—*Description of Keen's crown-vigor classes*

Character	Class A	Class B	Class C	Class D
Crown vigor	Full, vigorous	Good to fair	Fair to poor	Very poor.
Crown length	Long, 55% or more of total height; or less only if more than average width.	Average length, less than 55% of total height (approximately 30% to 55% if full and wide), or a longer crown if narrower or somewhat thin.	Short (from 10% to 30% of height, if crown of normal density) or long, sparse, and narrow.	Very short (less than 10% of total height), sometimes merely a tuft at top of tree, or somewhat longer when sparse and ragged.
Crown width	Usually average width or wider (narrower if very long and dense).	Usually average width or narrower; may be flat on one side.	Usually narrow or flat on one or more sides.	Usually very narrow and sparse, or limbs all on one side.
Crown density	Usually full and dense or of medium density if longer than 55%.	Usually of full to medium density, not sparse or ragged.	Often sparse and ragged except at very top.	Sparse and ragged.
Foliage	Needles of average length or longer, usually dense and thrifty.	Needles of average length, usually dense and thrifty.	Needles often short and thinly distributed, but of normal length and density when confined to top one-third of crown.	Needles often short, foliage sparse or scattered or only partially developed, but of normal length if reduced in quantity.
Position	Usually isolated or dominant, rarely codominant.	Usually codominant; sometimes isolated or dominant; rarely intermediate.	Usually intermediate; sometimes codominant or suppressed, but rarely isolated or dominant.	Usually suppressed or intermediate, but may occupy other positions if greatly reduced in vigor.
Diameter	Large for age	Average or above for age	Usually below average for age; sometimes larger in decadent trees.	Decidedly subnormal for age, but very old, decadent trees may be of large diameter.

NOTE: The descriptions apply to the usual types of trees found in each class; where exceptions occur, the size of living crown and amount of foliage are the primary considerations in determining the vigor class.

Portland, Oreg., and the data were analyzed by P. A. Briegleb of the Pacific Northwest Forest and Range Experiment Station to determine growth rate by Keen tree classes (*10*, *11*).

Results showed of the study that diameter growth rate was closely associated with Keen tree classes. Diameter growth decreased progressively with age from 1 to 4 and with crown class from A to D. Thus Tree Class 1A showed the greatest diameter growth, Class 4D the least. This explained why certain of the tree classes, representing trees of poorest growth, could be used in judging tree susceptibility. The use of this system of tree classification in timber marking for the removal and salvage of susceptible trees as a measure for the indirect control of the western pine beetle is discussed in Section V, p. 335.

Tree-Class Slide Rule

As a further help in standardizing interpretation of the various Keen tree classes, especially for borderline and atypical cases, Keen (*73*)—with the help of J. M. Whiteside and R. C. Grant—developed a tree-class slide rule that put the essential factors of tree classification on a rule-of-thumb basis and gave proper weight to each of the more important elements.

The construction of the tree-class slide rule was based on a statistical analysis of 3,611 trees examined in 1939 on fourteen 10-acre plots scattered through eastern Oregon. The crown-vigor rule integrated the factors of crown length, crown width, and density. These were modified for spike-topped or suppressed trees. The tree age or relative maturity rule was based on an integration of percent of black bark (fissured, fast-growing, young bark) and tree diameter at breast height, modified by site and crown class.

Field tests over a period of more than 10 years in eastern Oregon, where it was primarily applicable, showed that the slide rule was reliable in determining the proper tree classification for individual ponderosa pines, particularly in respect to their age or maturity class.

Risk Rating

Although tree classes were found to be a tremendous aid in differentiating susceptible and nonsusceptible types of trees in ponderosa pine sands, these systems did not entirely solve the problem of recognizing those trees most likely to be attacked at an early date. This was pointed out in an article by Keen and Salman (*82*):

> While this tree classification indicates in a general way which types of trees in a virgin stand are most susceptible to bark bettle attack, and therefore the kind of tree representing the highest risk of loss over a long period of years, it does not show which individual trees are likely to be killed within any short period of time.

Risk ratings were developed as a result of attempts to control the western pine beetle by light selective cuttings that would remove those trees most likely to be attacked by beetles within a few years.

The primary objective of the selective cutting was control. Therefore, it was desirable to make a cut no heavier than necessary to reduce the immediate beetle hazard. The problem requiring solution on Blacks Mountain Experimental Forest was explained by Salman and Bongberg (*121*) as follows:

> When the Blacks Mountain Experimental Forest was established in 1934, a preliminary light sanitation cut which would remove a relatively small percentage of the total merchantable volume was planned by the California Forest and Range Experiment Station. Foresters selected trees for cutting entirely on the basis of their high silvicultural undesirability. During the winter of 1934–35 serious infestations were found to be present throughout the experimental area, and it was observed that the greater portion of the loss occurred in trees that had not been marked for removal in the sanitation cut. . . . It became evident that special criteria should be used in the selection of trees if a light cut was to be successful in reducing losses due to insects.

The characters distinguishing four classes of risk for grouping all merchantable trees in the stands were first described in a memorandum by Salman (*U276*). Redefinition and publication was made by Salman and Bongberg in 1942 (*121*). (Fig. 41 and table 5). A colored plate illustrating the risk classes was published by Whiteside (*150*) in 1951.

Characteristics of crowns were used almost entirely in separating trees into four groups of low, moderate, high, and very high risk. In particular, needle color, needle complement, and degree of twig and branch killing were used as a basis in judging risk. To some extent, these four risk groups paralleled Keen's four vigor classes A, B, C, and D, which also rated crown vigor largely on the basis of quantity of foliage, density, color, and general thrift. This similarity in the two systems caused a great deal of confusion at first, and still does.

The difference in the systems is essentially one of distinguishing inherent vigor (Keen's classes) from current health (risk ratings). This is quite impossible to do for trees of normal vigor and health, but becomes important in recognizing trees currently declining in health or sick from one cause or another. Trees of highest risk were those in risk 4 which were obviously in a poor condition of health as indicated by short, sparse, off-color foliage, and dead or dying twigs and branches.

Because the risk rating of ponderosa and Jeffrey pines had an immediate and highly practical application in indirect control of the western pine beetle and the Jeffrey pine beetle, studies were pressed from 1937 to 1943 to further define risk characters and to improve the methods of distinguishing high-risk trees.

In the first tests of risk rating, made on the Blacks Mountain project in 1937, Bongberg (*U22*) found that high-risk trees were quite evenly distributed over the area and occurred in practically all diameter classes (fig. 42). They were more abundant, however, in the predominating diameters of the stand.

In 1938, Bongberg (*U23*) attempted to measure crown characters that denote risk, particularly the complement or number of fascicles

FIGURE 41.—Degrees of risk in ponderosa pine.

per twig and the length of the needles. He found that thin crowns of high-risk trees averaged 48 fascicles per twig, while dense crowns of low-risk trees averaged 121 fascicles. Needle length ranged from 4.2 inches on high-risk trees to 7.1 inches on low-risk trees.

In 1940, Hall (*U83*) studied the physiological factors associated with crown decadence on eight trees and concluded that:

> There are certain measurable factors in the crown of a tree which are indicative of marked decadence. These include greatly reduced twig increment for a period of about eight years, shortened needles, and fewer needle fascicles.

The measurement of crown characters that indicate degree of risk was investigated quite thoroughly by Wygant (*U338*) at Blacks

TABLE 5.—*Descriptions of risk ratings*

Risk rating	Symptoms
Risk I—Low risk	Full-foliaged, healthy-appearing crowns. Foliage of healthy appearance, needles usually long and coarse, color good dark green. Practically all twigs with normal foliage complement. No weakened parts of crown.
Risk II—Moderate risk.	Fair to moderately healthy crowns, imperfect in spots. Foliage mostly healthy, needle length average or better, color fair to good. Some twigs or branches may lack foliage, but such injury should not be localized to form definite "weak" spots in crown.
Risk III—High risk	Crowns of fair to poor health, somewhat ragged or thin in parts of crown. Foliage in parts of crown thin, bunchy, or unhealthy, needles average to shorter than average in length, color fair to poor. Some to many twigs or branches lacking foliage, some to many twigs or branches fading or dead. Small localized weakened parts of crown usually present.
Risk IV—Very high risk.	Crowns in poor condition, ragged or thin, often showing evidence of active insect infestations in upper parts. Foliage thin or bunchy, needles short or sparse, color poor. Twigs and branches dead or dying, parts of crown definitely weakened. Active top-killing or partial infestations often present.

Mountain during 1941. Seventeen high-risk trees and 16 low-risk trees were felled and analyzed to determine differences in needle length, needle diameter, needle retention, needle complement per twig, twig growth, and radial diameter growth. The more significant results brought out by this study were stated as follows:

The average needle complement per twig in the top and mid-crown of the risk 1 trees was 69 percent better than that on the risk 4 trees. This difference between the risk 1 and risk 4 trees was very highly significant, and between the risk 1 and risk 2 trees not significant. The variation in the number of needles per twig from tree to tree within each risk class was great.

The average needle length in top and mid-crown of the risk 1 trees was 29 percent greater than on the risk 4 trees . . . The variation from tree to tree within each risk class was great. . . .

The average annual twig growth in the top and mid-crown during the past 25 years of the risk 1 trees was 32 percent better than that of the risk 4 trees. This difference in growth was very highly significant. The variation from tree to tree within each risk class was great.

Twig growth on the risk 4 trees has been on a decline throughout the past 25 years. While the growth on the risk 1 trees has been on somewhat of a decline during that period, the risk 1 trees have shown recovery since 1936 not shown by the risk 4 trees. At no time during the 25 year period did the twig growth of the risk 4 trees equal that of the risk 1 trees.

The average annual radial growth during the past 30 years at the mid-bole of the risk 1 trees was 46.5 percent greater than at the stump. Mid-bole growth on the risk 4 trees was 11.1 percent

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FIGURE 42.—Painting spots on ponderosa pine to denote degrees of risk to western pine beetle attack. Blacks Mountain Experimental Forest, Calif.

less than growth at the stump. Literature on tree growth indicates that annual radial growth on the stem is normally greatest just below the living crown. Therefore the risk 1 trees were growing in a normal manner and the risk 4 trees were growing in an abnormal manner.

Radial growth has been on a decline throughout the past 30 years. This decline has been greater on the risk 4 trees than on risk 1 trees. The risk 4 trees failed to show the improvement in growth that risk 1 trees have shown since 1936. (Fig. 43.)

The fact that Wygant found differences in twig growth and annual radial growth for periods of 25 and 30 years between the two groups of trees studied shows conclusively that he was dealing with long-time tree class differences rather than short-term current health differences.

Wygant (*U339*) also found that ocular estimates of needle complement per twig and needle length are subject to considerable error. In general, appraisals were found to be between 64 and 68 percent correct. Apparently the appraiser is influenced in estimating needle length and needle complement by his general impression of the tree's vigor.

In 1940 Bedard (*U12*) made an analysis of the crown and other characters in high-risk trees in southeastern Oregon:

Seven characters were found to be associated with high-risk trees. These were: (1) scraggly, scattered, open crown, (2) thin open top, normal or dense below, (3) very thin open crown through-

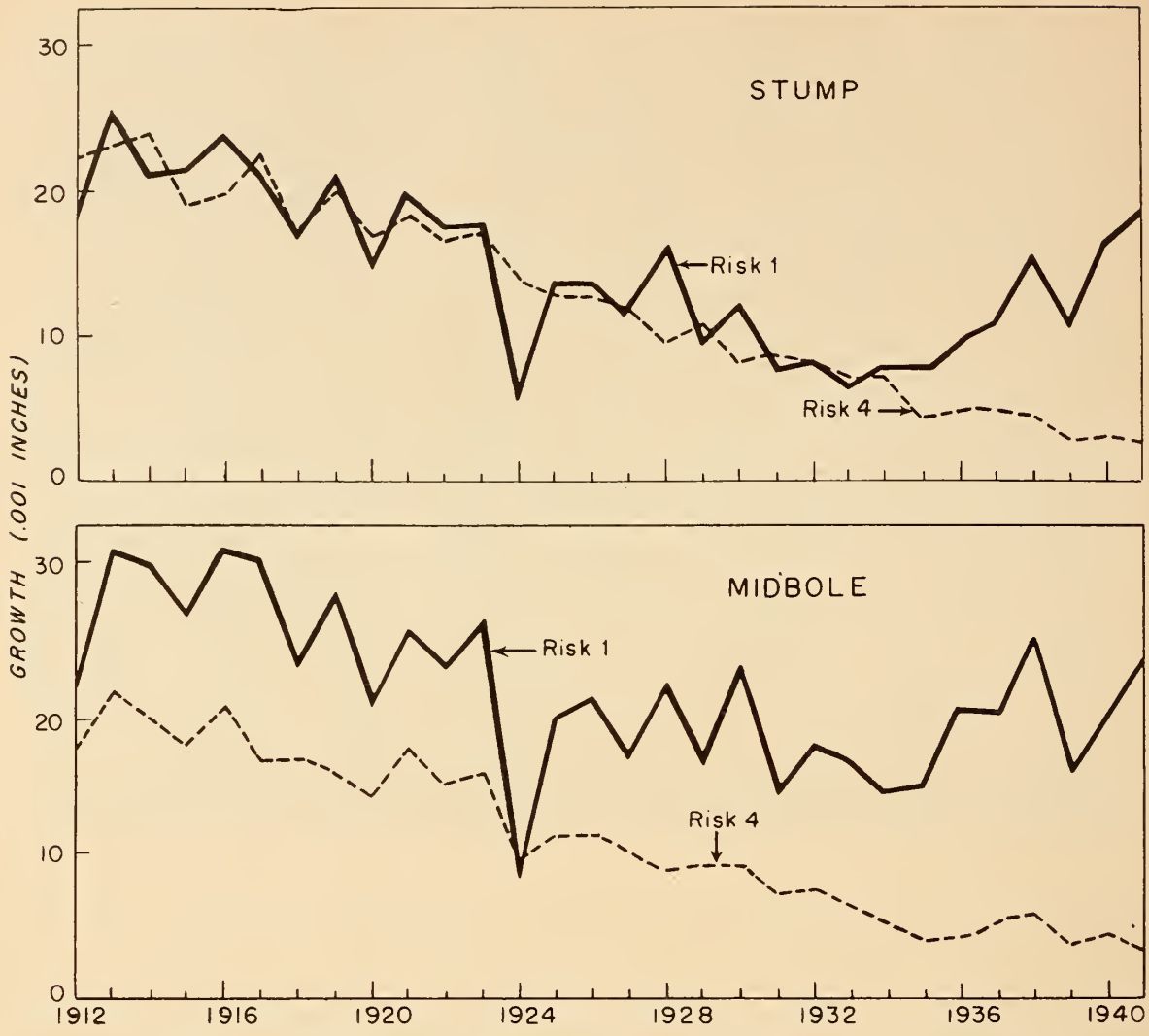

FIGURE 43.—Comparison of annual radial growth of Risk 1 and Risk 4 trees.

out, (4) very short needles in top of crown, normal below, (5) new spike, newly broken top, or active area below an old spike, (6) medium wide active sapwood, and (7) abrupt growth declines with no recovery.

By the close of the 1941 season, Bongberg (*U27*) was able to check the reliability and significance of risk characters in 58 trees that had died after risk rating on 15 sample plots of the Blacks Mountain area. He found that a sparse complement of needles in the top crown, in contrast to a more dense foliage below, was the most reliable and valuable character indicating high risk; that short needles alone were of little value; that severe branch and twig injuries were of limited value; and that top injury is of definite value as a character in appraising high risk.

During 1943, Bongberg (*U30*) reviewed the mortality that had occurred in high-risk trees on sample plots at Blacks Mountain during the period 1937–43. His material consisted of 556 ponderosa and Jeffrey pines (557,300 board feet) killed from 1 to 6 years after the trees had been rated according to risk. The records showed that

62 percent of the trees were rated as Risk 4 and were classified in the overmature Class 4 of Keen's tree classes. The study also showed that if all Risk 4 trees were taken out of the stand, the remaining loss would show little difference in ratio of mortality by Keen's crown vigor classes. In his summary, Bongberg stated:

> By comparing the percent of risk class killed each year and for the entire period of record with the percent of occurrence of the green stand by risk, it has been found that mortality ratios for each risk class are significant. This comparison also showed that the risk ratings are applicable to both ponderosa and Jeffrey pine under infestation conditions (annual loss) ranging from 0.03 to 0.99 percent of the green stand, and can be used in predicting future loss for at least six years. . . . It was found that maturity was of little value as an added factor to ratings of risk . . . but that the preponderance of risk trees occur in the overmature age classes.
>
> The ratio of mortality or relative susceptibility of trees was found to be greatest in Keen's susceptible tree classes . . .

In connection with the Rail Glade test of sanitation-salvage logging in Bly District, Oreg. (see Section V, p. 342), a nearby sample plot of 640 acres was not cut and high-risk trees were marked on it in 1940 under the same rules used on the logged area. The purpose of the test marking was to determine (1) what proportion of beetle-killed trees could be selected in advance of an attack, and (2) what proportion of trees marked for cutting would be actually killed over a 5-year period (*U160*).

Bedard (*U20*), summarizing the first 3 years' results of this study, showed that 67 percent of the volume and 55 percent of the trees that were killed occurred in that part of the stand (approximately 15 percent) that was marked as high risk. The remainder of the loss (45 percent) occurred in unmarked trees that were not recognized as high risk. The proportion of loss in marked trees compared with total stand loss varied by years and by seasonal generations. It appeared that as the infestation declined, a higher percentage of the total loss occurred in high-risk trees; with higher levels of loss, a larger proportion of the low-risk trees were attacked and killed. But in the 3 years, only about 10 percent of the marked high-risk trees had been killed.

This test showed that it was not possible to select a high percentage of trees that might be killed by western pine beetles in advance of their attack without also selecting many trees that would normally survive. In another instance, on twenty-two 10-acre sample plots in eastern Oregon risk rated in 1941 and 1943, 409 trees were rated as Risk 4 (*U166*). Of these, 124 or 30.3 percent were killed by insects; 10 were cut in logging or felled by wind; and 275 or 67.2 percent were still living 10 years later. While 44.5 percent of the 10-year loss on these plots occurred in the Risk 4 group, over two-thirds of this group survived a 10-year period. Thus it is incorrect to assume that all Risk 4 trees are doomed to die within the next decade. Also, on these 10-acre plots carrying 6,535 trees, 1,280 were rated

as Risk 3 and 4. Of these, 187 trees or 14.6 percent were killed by insects in the next 10 years and 1,093 or 85.4 percent survived. If all Risk 3 and 4 trees had been cut in order to save 187 trees that would have been insect-killed, 1,093 trees would have been cut that would have survived a 10-year period.

On the Rail Glade experiment, as on other tests of sanitation-salvage, a higher proportion of selected trees was killed than the general average of killed trees in the stand. While only 67 percent of the total volume of loss was predicted in the selection of risk trees under undisturbed conditions, the removal of such trees through sanitation-salvage logging was much more effective as a control measure than might be expected. It resulted in over 90 percent reduction in infestation. This was probably due to the removal of "key" trees from groups and weak trees that would have served as sources of infestation.

Penalty System of Rating Risk

Under the California risk-rating system (*121*), ponderosa or Jeffrey pines are divided into four categories: Risk 1 and Risk 2, the normal or nearly normal low-risk parts of a stand comprising from 75 to 85 percent or more of a typical virgin pine stand; and the risk element—Risk 3 and Risk 4—normally comprising from 15 to 25 percent of the stand. While the risk element can be arbitrarily placed in these two classes of high and very high risk, actually there is a gradation of risk from low through moderate to extremely high risk for individual trees.

Since in sanitation-salvage cutting we are not concerned with normal parts of a stand, the idea developed of ignoring this large part and confining attention to trees that were below par from one or more causes. In 1941, Keen proposed that trees be given a penalty score for each condition of poor health and that the sum of the penalty scores would thus indicate the degree of risk. With the late W. D. Bedard cooperating, a score card was developed for the penalty points to be assessed against a tree for each abnormal condition indicative of risk.

The penalty points were based on assumed mortality ratio for each abnormal condition. The penalty for poor crown condition (up to a maximum of 4 points) plus the penalty for poor needle condition (also up to 4 points) plus penalties for weakness or injury (up to a maximum of 8 points) gave the total penalty score for each tree. Thus the maximum penalty that could be imposed was 16. Penalties between 3 and 5 were considered about equal to the California risk rating of 3, while a penalty score of 6 and over would be a Risk 4 tree.

The "penalty system" of rating risk was first tried in 1941 on the Swede Cabin sanitation-salvage control test, Bly District, Oreg. (see Section V). The penalties weer revised in 1942 at a conference of timber markers and forest entomologists at Seneca, Oreg. (table

6). Although the penalty system rapidly became a useful tool, particularly for training purposes, it was not published until 1944 (*13*).

J. W. Bongberg, in collaboration with T. J. Orr and C. Borsting of the Weyerhaeuser Timber Company at Klamath Falls, Oreg., developed a new set of penalty scores in 1949 particularly adapted to marking some experimental cutting areas north of Bly, Oreg. Trees with penalty scores of 9 or more were considered of high risk and were marked for cutting. In 1950, this penalty scoring system, with some modifications (table 7), was applied to a cutting made at Pringle Falls Experimental Forest by the Pacific Northwest Forest and Range Experiment Station. It was first published by Sowder (*122*) in his report of the experiment. Since then, this scoring system has been adopted by several other timber markers in the Pacific Northwest.

TABLE 6.—*Penalty system of rating tree risk* [1]

Symptoms of poor tree health	Penalties	
	Moderate condition	Bad condition
I. *Crown Condition* (Score 0 to 4).		
1. Weak spots in crown	0	1
2. Scattered, scraggly, irregular crown	1	2
3. Thin open crown throughout	1	2
4. Thin open top, dense below	2	4
5. General poor vigor, unhealthy	2	4
II. *Needle Condition* (Score 0 to 4)	0	1
1. Tufts at end of long bare branches	0	1
2. Complement below average	1	2
3. Length below average	1	2
4. Short needles in top, longer below	2	4
5. Fading or off color	2	4
III. 1. Mistletoe or witches' broom	0	1
2. Old spike not active	0	1
3. Broken top, not dying below	0	1
4. Fire scar	0	1
5. Dying lateral twigs	0	1
6. Dying tip of terminal	1	2
7. Lightning strike	3	6
8. Active top killing	4	8
9. Active infestation (*D. brevicomis, D. monticolae, D. valens,* and other insects)	6	8

[1] Original by F. P. Keen (1941); revised at Seneca conference (August 1948).

Relation to California risk rating:

Risk rating	*Penalty Score*
1	0.
2	1–2 inclusive.
3	3–5 inclusive.
4	6 and over.

TABLE 7.—*Penalty system for rating high-risk trees* [1]

Symptom	Penalty
A. *Needle condition.*	
(1) *Needle complement* (number of needle fascicles per twig).	
Less than normal complement throughout crown. No contrast evident in complement between upper and lower crown	2
Thin complement in upper crown; normal complement in lower crown. Contrast in complement evident between upper crown and lower crown	4
(2) *Needle length* (length of individual needles).	
Needles shorter than normal throughout crown. No contrast evident in needle length between upper crown and lower crown	2
Needles short in top; normal length below. Contrast in needle length evident between upper crown and lower crown	4
(3) *Needle texture* (apparent weight of needle—coarse or fine).	
Light needles throughout crown. No contrast in texture evident between needles in top crown and lower crown	1
Feathery needles in top crown; normal or light texture in lower crown. Contrast in texture evident between top and lower crown	2
(4) *Needle color* (green color of needles).	
Needle color light green—lighter than normal green	1
Needles definitely off color	2
B. *Twig and branch conditions.*	
(1) A few scattered dead or dying twigs or branches in crown	0
(2) Many scattered dead or dying twigs or branches in crown	1
(3) Severe scattered dead or dying twigs or branches in crown	2
(4) Severe dead or dying twigs or branches in crown that form a definite weak spot or hole in crown, particularly in top ⅓ of crown (localized weakness)	3
(5) Severe dead or dying twigs or branches in crown forming more than one weak spot in crown, particularly in to ⅓ of crown (localized weakness)	5
C. *Top crown condition.*	
(1) Old top-kill where there is no progressive weakness or killing in green crown below	2
(2) Old top-kill and a progressive weakness or killing in green crown below	4
(3) Old spike where there is no progressive weakness or killing in green crown below	1
(4) Old spike and a progressive weakness and current killing of limbs and branches below	5
(5) Long bare spike (⅓ or more of total stem length) which leaves only a few widely spaced green branches in crown	6
D. *Other factors.*	
(1) Keen tree classes. All C and D crowns	2
(2) Lightning strikes:	
Currently struck	9
Old strike (healed)	1
(3) *Dendroctonus valens* attacks in basal bole:	
current	6
old, pitched out	2
(4) Broken tops:	
Current break leaving only a few branches on the bole	9
Old break and new terminal starting	0
(5) Mistletoe:	
Heavy witches' broom	1
Canker on stem	5

See footnotes at end of table.

TABLE 7.—*Penalty system for rating high-risk trees* [1]—Continued

Symptom	Penalty
D. *Other factors*—Continued	
(6) High-risk trees in group of other trees which might serve as a focal point for infestation of entire group	3
(7) Fire scar 50 percent or more of circumference or basal area which indicates progressive deterioration of wood (mechanical risk)	3
(8) Hot spot—where tree is located in the midst of large group of snags indicating that group has been killed gradually over the years	1
(9) Mistletoe in smaller diameter trees.[2] Very heavy mistletoe witches' brooms and where the crown excluding the witches' brooms would be D crown	9

[1] Set up in 1949 by Jack W. Bongberg, Forest Insect Laboratory, Bureau of Entomology and Plant Quarantine, Berkeley, Calif., and Thos. J. Orr, Forester, Weyerhaeuser Timber Co., Klamath Falls, Oreg.; later modified slightly by James E. Sowder, Pacific Northwest Forest and Range Experiment Station, Portland, Oreg. First reported by Sowder (*122*).

[2] Not necessarily a high-risk tree from the entomological point of view.

Taking into account the mortality ratios obtained from a 10-year record of actual ponderosa pine mortality on twenty-six 10-acre virgin pine plots in eastern Oregon, Keen (*U166*) proposed a new penalty score system in 1954 (table 8). In this system, five categories are recognized with a total possible score for each as follows:

I. Crown condition	6
II. Top condition	8
III. Needle condition	10
IV. Twig and branch injury	8
V. Other weaknesses or injury	6
Total possible penalty score	38

Any tree with a penalty score of 5 or more would be considered high risk; one with a score of 9 or more would be of very high risk.

Change in Risk

Since degree of risk is a relative expression of current tree health, it can be expected that risk ratings in individual trees may change over a period of a few years as trees respond in health and vigor to changes in precipitation and other factors affecting their growth.

Salman (*U278*) found that risk ratings of a few trees on the Blacks Mountain Experimental Forest were changed in 1940 by the effect of a needle cast fungus and the generally short needle growth of 1939.

Employing photographic methods, Eaton (*U54*) began a study in 1940 of the change of risk of 48 trees on the Blacks Mountain area. Pen and ink sketches were prepared to illustrate the overall appearances of four classes of risk (fig. 40, p. 178). In 1953, the 13-year changes in risk were studied by Furniss (*U62*) who found that, except for 11 high-risk trees killed by bark beetles, most of the rated trees had improved in appearance. During this study period there

TABLE 8.—*Penalty score for rating tree risk* [1]

Symptom	Penalty	
	Moderate condition	Bad condition
I. *Crown Condition* (Score 0–6).		
1. Thin; weak-spot below top	0	1
2. Thin foliage bunched at end of long bare branches	0	1
3. Thin crown throughout	1	2
4. Scattered, scraggly, open crown	1	2
5. Thin open top; dense below	2	4
6. Very thin open crown	3	6
II. *Top Condition* (Score 0–8).		
1. Weak, stagnant top	0	1
2. Weak, thin, pointed top	1	2
3. Old spike top (not active)	1	2
4. Broken top (not active)	1	3
5. Dying tip of terminal	2	4
6. Declining vigor in top	3	6
7. Active spike or top-killing	4	8
III. *Needle Condition* (Score 0–10).		
1. Complement below average	0	1
2. Length below average	1	2
3. Very short in top; normal below	2	4
4. Very short, small complement	3	6
5. Fading or off color	4	10
IV. *Twig and Branch Injury* (Score 0–8).		
1. Lateral twigs dying	1	2
2. Lateral twigs and branches dying	2	4
3. Lateral twigs and branches dead and dying	4	8
V. *Other Weakness or Injury* (Score 0–6).		
1. Fire scar	0	1
2. Lightning strike	3	6
3. Mistletoe	0	3
4. Witches' brooms	2	4
5. *Dendroctonus valens* attack at base	1	4

[1] Keen's revised penalty score of 1954 based on 10 years of mortality experience on twenty-six 10-acre plots in virgin ponderosa pine stands of eastern Oregon (*U166*).

had been an upward trend in precipitation and it was believed that this improvement in moisture was largely responsible for the decrease in risk ratings.

During almost the same period, from 1941 to 1953, Keen (*U166*) found a marked improvement in risk for 6,000 tagged trees on twenty-two 10-acre study plots in eastern Oregon. While there was no significant change in tree class, he found:

> There was a noticeable change in risk ratings, however, with 62 percent the same, 32 percent with better ratings, and 6 percent with poorer. This confirms the general impression and the loss record, which showed that the stands on these plots had improved in health and vigor.

This improvement also coincided with an improvement in moisture and growth conditions on the Oregon plots.

Accuracy in Duplicating Tree Classification

Many trials have been made to determine how well different workers can duplicate the classification of a given set of trees on different occasions, and how well a number of trained men can classify trees in agreement with a standard. Trials have been run at ranger training schools, at spotter training camps, and in special tests between trained workers. The classifications that have been compared are Dunning's, Keen's, and risk.

The accuracy of duplicating any classification depends upon the training and experience of the men using it, the number of classes in the system, and the preciseness of class definitions.

Because of its 16 classes, Keen's tree classification offers the greatest chance for error in replication. But if this classification is broken down into the two primary subdivisions of age and crown vigor, each of which has only four subdivisions, then a higher frequency of agreement should be obtained. Dunning's classification with seven classes should represent the next most difficult classification to duplicate, and the risk classification with four classes should be the easiest.

Eaton (*U55*) compared the individual ratings of five men for the same trees on the same area in 1941 and found considerable variation in results. In a plot of 100 trees, each tree was classified visually according to Dunning, Keen, and risk. The ratings varied not only between individuals but also between first and second classifications by the same man. Eaton found the average frequency of agreement among the three most experienced observers, classifying the same trees on two occasions 2 weeks apart, was as follows: Dunning, 78 percent argreement; Keen, 82 percent agreement in age, 72 percent agreement in crown vigor, and 60 percent agreement in both; risk, 73 percent agreement.

The frequency of agreement with a standard rating (the first rating of the most expert man) for Dunning and risk was as follows: Dunning, 83 percent agreement; risk, 60 percent agreement. Keen's system was not included in this test.

Eaton states:

> The ability of a marker to classify trees uniformly varies with his experience . . . Ratings applied to the same tree by men of equal experience compare favorably, but untrained men cannot satisfactorily apply tree classes guided only by published descriptions of the systems.
>
> Discrepancies in the tree class ratings made by different men may be accounted for by the fact that the discernment of the characters is not critical. Characters, like crown length, that may be compared against a standard, are more consistently rated than characters like twig injury, that cannot.

Rangers and insect survey crewmen at training schools in Oregon and Washington have frequently been tested to determine their

accuracy on rating a series of 73 to 200 trees by Keen's tree classification. The results were as follows:

Men tested:	Year tested	Trees (number)	Agreement in tree-class ratings: By age (percent)	By vigor (percent)	Both age and vigor (percent)
37 rangers	1935	73	73	65	50
15 insect survey crewmen	1937	200	85	90	62
12 insect survey crewmen	1939	200	86	74	63
3 trained forest entomologists	1939	200	80	70	56
3 trained forest entomologists	1943	100	85	80	68

Experience has shown that tree age can be much more accurately judged than crown vigor class and that slight variations in either tend to operate against obtaining a high percentage of agreement when 16 classes are involved. From all of the trials so far, the average accuracy in duplicating Keen's classification and risk ratings is as follows:

Keen's classification:	Categories (number)	Agreement (percent)
By age	4	80
By crown vigor	4	72
By both age and crown vigor	16	60
Risk ratings	4	72

Relation to Silvicultural and Environmental Conditions

In addition to studies of the characteristics of the host tree and its susceptibility or resistance to western pine beetle attack, several other lines of investigation have been concerned with the influence of the environment and silvicultural characteristics of the forest stands in which most damage occurs. Climatic, edaphic, environmental, and forest stand factors have been studied for clues that might throw some light on the reasons for the rise and fall of epidemics. An understanding of these factors is basic to control of the beetle through forest management practices.

Climatic Factors

Precipitation

Soil moisture, largely determined by the volume of seasonal precipitation, is a dominant factor in ponderosa pine growth. Since insufficient moisture restricts growth and lowers tree resistance, it is only natural that periods of drought have been suspected as underlying causes of epidemic bark beetle activity. Hopkins (*44*), however, was not impressed with the importance of this factor, since he included the western pine beetle in the following generalization: ". . . drought is not an important factor in contributing to the multiplication or destructiveness of this class of enemies." On the other hand, Craighead (*22*) found a direct correlation between rainfall deficiencies and epidemics of the southern pine beetle. Craighead and others advanced the theory that drought, through its effect in lowering the growth vigor of trees, was partly responsible for outbreaks of the western pine beetle.

Increasing mortality of ponderosa pine in eastern Oregon after 1924, while charged to bark beetle attack, was suspected of being primarily caused by drought conditions and lowered tree vitality. Drought conditions were somewhat improved in 1927, and the rate of loss dropped the following year. More years of drought followed, and a most critical condition occurred in 1931 and 1932. Jaenicke (*U105*) reported that large volumes of timber on the China Hat sale area of Deschutes National Forest died primarily from drought. He stated:

> As early as 1931 it was clear that the drought factor was important in weakening the timber in the China Hat sale area and increasing its susceptibility to beetle attacks, but it was not until 1933 that much timber began to die primarily from drought. The drought killing now (January 1935) overshadows the pine beetle problem and further beetle protection has little or no chance for success because of the drought problem. Nearly all of the drought-killed trees are attacked by the western pine beetle, engraver beetles, and flatheaded borers, before the cambium finally discolors, but those insects are playing a secondary role in the timber losses now in progress.

To seek a correlation between precipitation and pine growth, Hauge (*U92*) used the records of the U.S. Weather Bureau station at Klamath Falls, Oreg., and selected cores from a stand of ponderosa pine within a mile of the station. Although this 1924 study was preliminary and limited in scope, Hauge reached the following tentative conclusion: "In semi-arid regions there is a high degree of positive correlation between the amount of precipitation and the rate of growth in yellow pine."

Many years of records were needed to establish evidence of cycles and the relation between precipitation and pine losses from bark beetles. Accordingly, Keen encouraged the continuation of plot loss records in the Klamath Basin of Oregon from 1921 over a period of more than 30 years, studying the rainfall-tree loss relationship as an integral part of the yearly pine beetle survey program. The trend of infestation in this area and the variation in seasonal precipitation at Klamath Falls and Lakeview, Oreg., are shown in figure 28, p. 134. While no direct relationship is evident, the heavy losses during the 1920's occurred during a time of general drought and the low losses since 1937 coincide with a more favorable precipitation period. A complete analysis of this long record is still to be undertaken.

In 1941 Hall (*U82*) compared average annual beetle-caused mortality in ponderosa pine on Modoc National Forest with the seasonal precipitation at the nearest permanent weather station (Lakeview, Oreg.) for the 1921–39 period. He was unable to find any evident relationship and stated: "The correlation between precipitation and timber loss is far from clear cut."

A discussion of the relationship between precipitation and pine losses on Sierra National Forest from 1909 to 1943 is found in a review of bark beetle investigations and control work by Miller, Struble, and Hall (*U209*):

> One characteristic of the association between precipitation and loss is that it is not specific in all years; i.e. a drought year does

not necessarily mean a heavy loss year, as may be noted for the years 1912, 1924, 1934, and 1939. Neither does above normal precipitation mean low loss as may be noted for the years 1914, 1932, and 1935 (see fig. 31, p. 137). In studying these data it appears that precipitation effects are cumulative, either favorable or unfavorable, and that precipitation effects in any one year are depedent to a large extent on precipitation for at least two years previously.

Although it can be shown that there is an apparent relation between precipitation and beetle populations as represented by pine losses, it must be conceded that the relationship is not a direct one. Obviously dry weather in itself does not generate beetles spontaneously; drought must first have an effect upon the trees which creates favorable conditions for the beetles to multiply.

A comparison of tree growth (radial) and precipitation, as represented by the average growth pattern of a series of selected trees from the Cascadel basin and the Northfork weather record for the period 1912–42, indicates that . . . the effect of precipitation on growth appears to differ in different periods; here again, as in the loss picture, the precipitation effect in any one year seems to be dependent upon precipitation in preceding years . . . The above normal precipitation for 1932 followed eight years when precipitation had been below normal and appears to have had no effect in changing the growth trend which still progressed downward in 1933. These data seem to show that the prolonged drought from 1924 to 1931 was a serious shock to the trees and that recovery after this drought was comparatively slow. From 1912 to 1931 the precipitation percent of normal was below the growth percent of normal in 17 out of 20 years; after 1931, however, the precipitation curve was above the growth curve in ten out eleven years.

In general it can be claimed that beetle-caused losses are inversely related to the growth rate . . . A steadily declining growth rate over a period of several years prior to 1930 was followed by a very rapid rise in the loss level; on the other hand, the general rise in growth rate from 1934 to 1940 was accompanied by a fluctuating, but nevertheless, substantial lowering of the loss level.

Climatic Cycles

A phase of the ecology of the western pine beetle which has received thorough investigation is the relation of tree-ring patterns to climatic cycles. Since it is generally accepted that several seasons of suppressed radial growth in pine stands are usually followed by periods of accelerated bark beetle activity, the regularity with which years of suppressed growth have occurred in the past should give a clue to the expectation of bark beetle losses in the future. Whether or not there is a rhythmic cycle of favorable and unfavorable growth years should show up in tree-ring patterns.

The tree ring record of the pine stands of eastern Oregon and northeastern California was intensively studied by Keen (*69*). Interest in this line of investigation was stimulated by prolonged droughts accompanied by increasing bark beetle infestations during

the years from 1917 to 1933. The application of the study was defined as follows:

> The question naturally arose in the minds of foresters and timber owners as to whether this trend toward dryness and retreat of the forest was to continue over any long period of time or was merely a short cycle in a variable climate which would soon reverse the trend and give some hope for forest perpetuation in threatened sites. Since this problem was intimately tied in with increasing timber mortality due to bark beetle activity, we, as entomologists, were concerned to know whether we could expect any eventual aid from Nature in holding beetle damage in check.

Mircrometer measurements showed annual radial growth in 1,240 ponderosa pines from 44 different localities in eastern Oregon covering a period of 650 years. The results were treated by statistical methods and served as the basis for the following conclusions:

> A significant correlation was found between seasonal precipitation and tree growth. On comparing the cumulative effect of two years of precipitation with tree-ring growth, a highly significant correlation ratio was found. By taking into account the distribution of rainfall through the year and the cumulative moisture through several seasons, an even higher degree of correlation may undoubtedly be found.
>
> The tree-ring record for eastern Oregon indicates that during the past 650 years there has been no general trend toward drier or wetter years. If such a trend exists, the change over a 650-year period is so slight that it is obscured by other fluctuations. Average growth for the 20-year period 1900 to 1919 was found to be identical with the average growth during the past 650 years. There have been important fluctuations in growth throughout the entire period, however, with alternate periods of good and poor growth.
>
> All tree-ring measurements agree in showing that a very critical subnormal growth period has existed since 1917. This slowing down of the growth rate is undoubtedly the result of deficient precipitation and lowered water tables. As compared with other drought periods, the present one is the most severe and critical that the present forests have experienced in the last 650 years. Several other periods have exceeded the present one in duration of subnormal growth, but none has approached it for severity. Growth in 1931, the poorest year, was 68 percent below normal.
>
> The tree-ring record indicates that the last period of 19 years of drought and poor tree growth represents a major fluctuation in a broad climatic cycle which eventually will be followed by a wet period of better than average growth. No rhythmic cycle has been found which would permit a prediction as to when this reversal in trend will occur.

Keen's article was published just before a series of wet years began in the pine areas in 1938 and continued without interruption by major drought years (except for 1939) through the winter of 1952–53. Mortality from the western pine beetle dropped during this period to less than 0.5 percent of the pine stand volume per year.

Light and Temperature

The three-way relationship between precipitation, growth rate, and western pine beetle losses is too complex to be stated by any simple formula. Other natural factors may influence growth rate and obscure the effects of precipitation, even though soil moisture is the dominant factor. Favorable light and temperature conditions are essential to normal growth; low temperatures may inhibit growth in years even when precipitation is abundant. Forest entomologists, however, have made few attempts to link the light and temperature factors into the chain of climatic influences that produces favorable growth conditions for the tree and indirectly increases its resistance to bark beetle attack.

Keen analyzed seasonal temperature variations in southeastern Oregon in an attempt to determine whether the incidence of epidemics was associated with abnormal temperature conditions. Nothing of any significance was uncovered in this study.

In a study of climatic factors, Hall (*U81*) found that zones of highest hazard from bark beetle attack are those where low precipitation, high temperatures, and rapid evaporation all combine to decrease available soil moisture. The temperature effect has not been isolated from the other factors.

Phenological Events

In principle, phenology deals with the timing of biological events—e.g., the opening of buds, emergence of insects from hibernation, or subsidence of insect activity in the fall—as these are related to latitude, longitude, altitude, and topography. It has been assumed that the differences between localities in timing of biological events can largely be accounted for by differences in the three or four basic factors.

Hopkins (*45*, *46*, *47*) developed what is known as "Hopkins' bioclimatic law," which he explains (*45*) as follows:

> The law is founded on the determined country-wide average rate of variation in the time at which periodical events occur in the seasonal development and habits of plants and animals at different geographical positions within the range of their distribution. Other things being equal, this variation is at the rate of four days for each degree of latitude, five degrees of longitude and 400 feet of altitude . . . later northward, eastward and upward in the spring and early summer and the reverse in the late summer and during autumn.

This law has been applied with some success east of the Rocky Mountains, but does not hold in the mountainous regions of the West.

Workers at the Ashland station collected a large amount of data pertaining to phenological events in the ponderosa pine type of the Rogue River area, Oreg., from 1914 to 1918. These records, showing the time when certain plant activities occurred at fixed stations, were kept in connection with seasonal history records of the western pine beetle. It was hoped that from this study it would be possible

to use the phenological events of certain plants as a key to the seasonal activity of bark beetles within the same area. All of the Ashland records were transmitted to Dr. Hopkins, who published (*45*) on the effect of altitude on beetle emergence (see Section I, p. 64) but did not include the records of plant activity as correlated with the beetles' seasonal history.

In the western pine areas, attempts to find a fixed relationship of plant and insect activity to elevation, latitude, and longitude have always encountered too many complications. In these areas there are many factors that modify the temperature conditions controlling plant and insect development. Slope, exposure, and the modifying effect of topography upon moist air currents from the Pacific create a very complex set of influences that do not lend themselves to simple analysis.

Phenological records from the Ashland area emphasized the extent of the departure from the theoretical constants of the bioclimatic law when these were applied to the varied climatic conditions of the Pacific coast pine region. In comparing emergence of the western pine beetle at elevations of 3,200 and 5,700 feet, the theoretical difference between sites was calculated to be 25 days but actual emergence records showed a difference of about 50 days.

No fixed relationship of western pine beetle activity to phenological factors has been established, because of the wide climatic and seasonal variations between localities within the range of the beetle's distribution (see Section I, p. 65).

Physiographic Factors

Elevation

Forest entomologists have frequently noted that an altitudinal range roughly coinciding with the optimum altitudinal range of the host tree appears most favorable for western pine beetle infestations. Above and below this range, conditions do not appear to be favorable.

Miller and Person (*U205*) were unable to establish broods in a pine stand 1,000 to 1,500 feet below the true ponderosa pine type in the southern Sierra. Usually epidemics are limited to the ponderosa pine belt below the 5,500 foot contour in this same region, even though a few ponderosa pines may be found at higher elevations. Keen (*U153*) used elevation as one of the criteria of hazard to bark beetle attack after he observed that the western pine beetle was less active and hand fewer generations at upper, colder altitudes than in the optimum range.

In 1939 Hall (*U81*) found that average daily air temperatures were approximately six degrees colder in the upper ponderosa pine zone at 5,000 feet than in the lower zone at 3,000 feet on the Burney area of northern California. Because of differences in temperature, the upper zone produced two and a quarter generations a year while the lower zone produced three and a quarter generations. Altitudinal differences in air temperature and soil moisture conditions, reflected in tree growth and resistance, are thus definitely correlated with degree of hazard to bark beetle attack.

Slope and Exposure

Struble (*U297*) said that "slope and exposure are important in limiting moisture supply during an endemic year, and influence the beginning of an attack in one locality in preference to another."

Salman and Johnson (*U286*) compared losses on north and south exposures and on slopes, flats, and ridges. They found that southern exposures were slightly more susceptible to losses than northerly exposures: Susceptibility indices were 1.08 and 0.92, respectively. Considerable differences, however, occurred between slopes, ridges, and flats: Ridges were most susceptible with an index of 1.95; slopes had an index of 1.40; and flats had the least loss with an index of 0.75.

Soil Conditions

The extent to which soil conditions may influence growth vigor and indirectly the susceptibility of ponderosa pines has been given only slight attention in western pine beetle studies. Bedard (*U13*) found that most of the literature regarding texture and structure of forest soils was confined to hardwoods, and that comparatively little is known about the soil requirements of ponderosa pine.

In 1928 Keen collected samples of the characteristic soils from mortality plots in the eastside pine type of northeastern California. No correlation was found between moisture-holding capacity and severity of ponderosa pine mortality.

Investigations of soil conditions were undertaken in 1938 as one phase of a general study of the influence of climatic and edaphic factors upon timber losses in eastside pine stands. Hall (*U81*) considered the main measurable soil factors affecting tree growth in this area to be (1) soil temperature and (2) soil moisture at varying depths up to 16 inches. Preliminary results indicated that "soil moisture at a depth of 9 inches was significant of the degree of beetle hazard, but that moisture at the surface and at a depth of 16 inches was not; soil temperature was apparently related to hazard."

From studies made in 1941 on a series of 13 irrigated and 13 nonirrigated trees, Bedard (*U16*) concluded that: "Irrigation increases the radial growth of ponderosa pines in years when precipitation is insufficient to supply normal moisture requirements." However, radial growth on the irrigated trees during the season of 1940 was no greater than on nonirrigated trees on the same site, indicating that these trees received sufficient moisture without irrigation.

In 1942 and 1943, Bedard analyzed the effect of chemical and physical properties of soil upon the growth of ponderosa pines. On small experimental plots, he controlled the amount of water, determined the wilting coefficients, and added nitrogen and phosphorus to test the effect of varying amounts of these materials. His summary (*U21*) of these experiments includes the following statements:

> Nitrogen affected top growth with increase in leader length, needle weight, needle complement, and top radial growth. Phosphorus resulted in increased twig elongation, needle length, needle weight, and both basal and top radial growth. In general these nutrients increased top growth and apparently tended to inhibit root growth—at least tops increased more in proportion than roots.

Water was the most dominant factor in these tests. An insufficient supply resulted in significant decreases in total growth. An optimum supply caused increased growth in twig elongation, needle complement, and basal radial growth. An additional supply above the optimum caused no additional growth increases. Water at or above the optimum did, however, cause tops to increase more in proportion to the roots.

The combinations of water and fertilizers showed no significant interactions generally except in a few cases when the component parts of the combination strongly supported or opposed each other. Nitrogen and water decreased top radial growth below the effect of nitrogen alone. Phosphorus and water decreased top radial growth but increased basal radial growth. The combination of all three shows these same interactions plus an additional increase in top over root.

Soil treatments had no effect on the growth period of shoot, needle, or cambium, except that water in insufficient quantities shortened the growing period.

Forest Stand Factors

Certain ponderosa pine stands are much more susceptible to western pine beetle attack than other stands, and repeatedly suffer heavier losses. Some areas over a period of years have cumulatively lost up to 90 percent of the original stand volume while nearby areas have suffered little or no depletion. The reasons for these differences have been the subject of much speculation, many theories, and some critical analyses of area and stand hazard factors.

Site

Differences in site were early suspected as a cause of differences between various forest stands in western pine beetle damage. As defined by the Committee on Forestry Terminology of the Society of American Foresters (*39*), site is "an area considered as to its ecological factors with reference to its capacity to produce forests or other vegetation, the combination of biotic, climatic, and soil conditions of an area." A favorable combination of these factors enables trees to produce vigorous growth and resist beetle attack.

No completely satisfactory method has been developed for measuring site for ponderosa pine. The standard practice has been to measure "site quality" by the optimum height of mature trees, "site index" by the height that trees reach at the age of 100 years. These measures of site, however, do not adequately integrate all of the ecological, biotic, climatic, and soil factors of an area. As a consequence, site and beetle behavior are not strongly correlated.

In terms of percent of stand killed, bark beetle losses over long periods appear heavier on low-quality sites than on high-quality sites. Some preliminary data were collected by Person (*111*, *U237*, *U242*), who concluded that: "In general, poorer sites with open pure ponderosa pine stands along ridges or on exposed locations are preferred by *D. brevicomis*."

In 1928 Keen (*U144*) studied the susceptibility within the Dunning tree classes of some 10,053 green and 13,160 beetle-killed ponderosa pines and analyzed the selection of these trees in relation to site. His conclusions were:

> Poor sites show a greater loss than good sites. On the poorest sites the selective tendency is less marked, the trees of all classes being reduced to such a low stage of vigor as to become susceptible to attack. On good sites there is a marked selection of the suppressed and codominant trees of (Dunning's) classes 4 and 7. As the site becomes poorer the proportion of loss increases in the dominant classes 1, 3, and 5 and decreases in the codominant, intermediate, and suppressed classes 2, 4, 6, and 7.

In 1935 Keen (*U151*) summarized the loss records from 15,680 acres of sample plots cruised in southern Oregon and northern California during the 12-year period 1921–32 to show the distribution of loss by sites:

Site:	*Average annual net board-foot loss per acre*	*Average percent of stand killed in 12 years*
3−	175	10. 8
4+	232	14. 6
4	298	27. 8
4−	280	34. 0

According to Keen, this table:

> . . . indicates that insect losses bear a definite relationship to site quality either directly or indirectly. The percent of stand killed increased with a decrease in site quality. The net loss in board feet per acre, however, was somewhat lighter on Site 4— because of the smaller volume of the stand on such a site.
>
> And yet, the above averages only tell a part of the story, for in some cases relatively poor sites have shown very low losses, while some good sites have sustained extremely high losses. The rate of tree growth and the degree of individual tree vigor is frequently independent of site quality and appears to play an important part in determining susceptibility in any particular stand. It is necessary, therefore, to look further than site quality for an index of bark beetle selection tendencies.

In a 1936 study of hazard factors in northeastern California, Salman and Johnson (*U286*) found that Site II has a susceptibility index of 0.93, Site IV an index of 0.88, and Site V an index of 1.27. They report: "The surprising thing about the susceptibility indices for the three sites represented in the sample is the relatively small spread between the indices for the markedly different conditions."

In 1937 a 10-percent count of snags was made on 174 half-section plots throughout eastern Oregon and Washington, showing the following comparative losses on different sites:

Site quality:	*Number of plots*	*Total snags*	*Average snags per acre*
II	2	980	1. 5
III	16	13, 000	2. 5
IV	137	109, 420	2. 5
V	19	17, 300	2. 8
All sites	174	140, 700	2. 5

This comparison shows very little difference in average number of snags per acre for the principal sites III, IV, and V. Other factors such as stand density, local precipitation, and infestation conditions apparently play a more important part in determining the intensity of losses than does the factor of site alone.

Keen (*U152*) made a multiple correlation analysis (*U152*) using 25 full-section plots in the Klamath Basin and their record of 10 years of losses. He showed a simple correlation coefficient between mortality and site index of —.65. This means that 42 percent of the variability in these losses was associated with site index. A partial correlation and "t" test showed that site had no significance in explaining losses when taken alone. In reference to this, Keen states:

> At first thought this is most surprising. We have been thinking of site and growth rate as highly important in explaining variation in losses and by this test they each fail to show significance.
>
> The reason for the failure of site index to show significance is partly due to the lack of spread in this case. Nearly all the plots ran to site quality IV and the total range in site index was only from 70 to 100. It is unreasonable to expect a variable that is nearly constant to explain any large part of the wide variation in losses. In the second place, site is at its optimum in the middle of the pine belt and decreases at both higher and lower elevations. Beetle losses increase at the lower elevations, but not at the higher and hence do not move together with changes in site.

In 1943 Bedard (*U17*) completed the analysis of a one-acre plot study started by Keen in 1938. Past ponderosa losses in terms of percent of stand killed were compared with various environmental and stand factors. No relationship between site and losses was shown in the simple correlation tests.

The conclusions from all of these studies indicate that heavy losses are frequently associated with the poorer sites, not because of the sites themselves but because poor sites are frequently associated with other factors more directly responsible for insect damage.

Volume Per Acre

The volume of timber per acre is another measure of site: In general, poor sites have low volume, good sites have high volumes. This factor has been considered as an index to stand hazard because many stands of low volume have suffered heavier losses than those of high volume.

In the multiple correlation analyses by Keen (*U152*), Keen and Grant (*U171*), and Bedard (*U17*), this factor showed strong negative relationship with stand mortality. Johnson's data (*56*) from northeastern California showed the same strong correlation between stand volume and beetle hazard zones.

Susceptible Volume

It would seem reasonable to expect that stands with the highest percentage of volume in susceptible trees should show the highest hazard to continuing beetle damage. Yet several multiple correla-

tion analyses by Keen and Grant (*U171*) testing susceptible volumes by Dunning's and Keen's tree classes failed to show this factor as having any significant positive correlation with loss. This was probably due to the strong positive correlation of susceptible volumes with total volume per acre. In Bedard's study (*U17*), the percent of susceptible volume showed a positive correlation with loss which almost reached the level of significance. Since such a low order of relationship was found between susceptible volume and loss, this factor could not be used in hazard analyses.

The proportion of high-risk trees in a stand has also been assumed to be a good measure of hazard. Percentage of high-risk volume (Risk 3 and Risk 4 trees) was used empirically in hazard-zonation work in California (*56*) as one of the principal indicators of hazard. It was also the major factor used in much of the hazard-zonation work in Oregon. In the correlation studies by Keen and Merriam (*U172*) of actual loss records on sample plots over a period of 20 years, the number of Risk trees showed a highly significant positive correlation (0.680) with the subsequent 10 years of loss. However, in the multiple correlations, the average weight to be given to this variable (16 percent) was much lower than three other variables, i.e., (1) past loss (54 percent); (2) volume per acre (25 percent); and (3) growth reduction (18 percent). These studies show that while this factor is significantly correlated with hazard, it is not nearly as important a factor as had previously been supposed.

Forest Type

Forest type usually changes with elevation and life zone. Ponderosa pine is characteristically a transition zone species. At the lower elevation fringe of the pine belt, it is often found in mixtures with mountain mahogany, juniper, and oak. Heavy losses of pine from beetles are frequently found in this fringe type (*U264*). Pure stands of ponderosa pine in the middle elevational zone are also often subject to heavy beetle-caused damage. At the upper elevational zones, the pine type occurs in mixtures with white fir, lodgepole pine, and other species. In these types, beetle damage is usually low, unless other species are competing seriously with pine for light and growing space.

Salman and Johnson (*U286*) found a low rate of loss where white fir was mixed with ponderosa pine in Lassen County, Calif., and a very high rate of loss where incense cedar occurred in mixture with the pine. They showed that the average percent of stand killed in 10 years by forest type was as follows:

Pine types:	*Susceptibility index*	*Average percent of stand killed*
Ponderosa pine, white fir	0. 68	21. 4
Ponderosa pine	. 72	19. 8
Ponderosa pine, Jeffrey pine	1. 01	25. 6
Ponderosa pine, Jeffrey pine, incense cedar	2. 02	33. 4

Obviously, no forest type can be permanently more susceptible than another without the pine ultimately disappearing from such a type. Therefore, the hazard of any forest type varies with time and with current forest conditions.

Density

The density of a forest indicates degree of competition which, if excessive, can be expected to reduce growth rate and tree thrift. But Bedard (*U17*) failed to show any significant relation between past loss and density of ponderosa pine, either by stems or basal area per acre. Johnson (*56*) showed a higher stand density on better sites, where the past loss and beetle-hazard ratings were low. Stands tend to be in balance with their environment, and only where sites have more stems than the ground can support would one expect to find heavy losses. This sometimes occurs in stands with a heavy understory of reproduction, either pine or fir.

Competition

Competition of brush, reproduction, or understory trees with mature pines has often been suspected of causing a weakening of the mature stand and increasing its susceptibility to loss. Bedard (*U17*) found significant positive correlations between loss and the percent of ground covered with brush. He also found a highly significant positive correlation with a competition index consisting of the percent of ground covered by reproduction times its average height. Because of great variability of competition on larger areas, this factor has not been found to be useful in hazard-zonation work.

Growth

Since growth rate of trees is a good indicator of their resistance or susceptibility, it was suspected that the relative growth rate of stands might be a measure of their hazard to beetle attack. Briegleb (*9*), studying selectively cut stands in Oregon and Washington, found that mortality, although variable, could be related to and computed from gross annual growth per acre in board feet. The relationship was curvilinear.

Keen (*U152*) found a highly significant simple correlation of —.76 between percent of stand killed and normal volume of growth on a study of 25 full-section sample plots in the Klamath Basin of Oregon. He also found an important comparison between the percent reduction in the last 10 years of radial growth and the previous normal, as these were correlated with loss. This proved to be the one outstanding factor indicating hazard when the partial correlation coefficients were tested.

Growth reduction also showed a high significance as a factor of hazard in the multiple correlation studied by Keen and Grant (*U171*), and was one of the important factors used in the construction of an alinement chart to determine hazard.

Cut-Over Lands

Since cutting affects density, competition, growth, volume per acre, and the percent of susceptible volume left in reserve, it is reasonable to expect that cutting will have a profound effect upon bark beetle damage.

Salman (*U269*) made a study of cut-over lands in the ponderosa pine type of California and found that except for lower volume, the losses followed the same general trends as in virgin stands. There was no marked change in the insects primarily responsible for loss. Losses were heavier on poor sites than on good sites, and heavier in pure pine stands than in mixed type. There seemed to be no relation of loss to methods of cutting, diameter distribution, or reserve volume. Losses were lighter on plots where the increment was high.

Yearly inventories of tree mortality on cut-over lands have shown that volume of loss is greatly reduced by cutting, but that the percent of stand killed per year may not vary greatly from nearby virgin areas. The trend of losses on cut-over lands follows the same trend as in virgin stands of the same locality. The effect of different methods of cutting in controlling pine beetle losses is discussed in Section V.

Area Hazard Studies

Forest entomologists recognize that all of the factors contributing to resistance or susceptibility do not operate singly in forest stands but rather in a complex and interrelated manner. The term "bark-beetle hazard" has been used to designate the net result of all the factors that contribute to the expectancy of western pine beetle infestations within a given area, and under the heading of hazard studies a large amount of research has been done.

Researchers observed that certain areas or zones were much more subject to recurrent losses than others, and it seemed obvious that site quality alone did not explain this differentiation. The age of stand, forest type, elevation, and various other factors might be used as equally suitable explanations. Nevertheless, it was believed that if pine stands could be classified, mapped, and inventoried according to the degree of hazard from beetle attack, the information would be of immediate value in forest utilization and management plans for specific areas.

Approaching the problem empirically, Salman and Johnson (*U286*) sampled a series of eastside areas in Lassen and Modoc National Forests in 1936 to determine whether physical characters of the stand would serve as indices to the rate of past, current, and expected losses; also to find out what practical difficulties would be involved in surveys to classify areas by degrees of hazard. The factors taken into account included stand volume per acre, timber type, site index, exposure, slope, relation of current to past losses, and thrift of trees as expressed by Keen's tree classes. It was found that the operation of all these factors was too complex to permit any simple method of weighing them in terms of beetle hazard. Among the conclusions reached in these preliminary studies were the following:

> It seems possible to secure a quantitative estimate of hazard by measuring the past loss if that measurement includes those that have occurred over a relatively long period of time.

The relative hazard also can be determined if one is experienced and has an intimate knowledge of past conditions by a visual estimate that takes into consideration the loss and certain gross environmental indices.

A combination of visual estimates and selected measured samples seems to be the more practical and satisfactory basis for securing a hazard rating.

An adequate quantitative and qualitative basis for rating hazard may be secured on a (1) general (subregional), (2) a fairly specific (environmental unit), or (3) a very specific (local environmental) basis. The second unit of estimate seems to be best adapted for the application in forest-management practice.

From these studies Salman and Johnson found that two factors bearing on current beetle hazard of pine stands were of particular significance: (1) the percentage of pine volume previously killed by bark beetles, and (2) the percentage of present pine volume occurring as high-risk trees. They proceeded to set up five classes of hazard ratings from very low to very high and developed methods for sampling and rating pine areas under this classification. These were the methods used for the hazard inventory of northeastern California pine stands begun in 1937 and completed in 1940 (see Section IV, p. 242).

Using methods of statistical analysis, Keen began a series of studies in 1938 in the eastside pine stands of Oregon to determine the principal indicators of hazard and the weights that should be given to each of the more important factors in order to integrate their total effect. The objective was to find a sound basis for making hazard zonation appraisals.

Keen (*152*), with the aid of R. C. Grant, made a multiple correlation in 1939 of 10 years of loss on 25 full-section sample plots in the Klamath Basin of Oregon with site index, volume per acre, volume of growth per acre, and growth reduction percent. Highly significant simple correlations were found between loss rate and all of these factors. A regression equation was developed that combined these factors and explained 51 percent of the variance in current loss. Of these factors, growth reduction was the most important and the only one to show significance in partial correlation tests.

Three more statistical analyses were made in 1941 by Keen and Grant (*U171*), using data from regional survey plots. Two different sets of data were used, combining different sets of factors. In the first analysis, using data from 25 full-section Klamath Basin plots, mean annual loss for the 10-year period 1931–40 (called "future loss") was correlated with past loss for the 10-year period 1921–30, susceptible volume by Dunning's classes, and radial growth reduction percent. This study showed a highly significant correlation between future loss and past loss and a highly significant negative correlation between future loss and susceptible volume per acre, but no significant correlation between future loss and past growth reduction.

The next analyses were based on data from 114 plots of 320 acres each scattered through eastern Oregon and Washington, plots on

which a stand inventory and snag count had been made in 1937. In these analyses, future loss (measured after the cruise) from 1937 to 1939 was correlated with past loss (before 1937), susceptible volume, total volume per acre, and growth reduction. It was found that future loss was significantly correlated with volume per acre and 1936 growth reduction, and highly significantly correlated with past loss. Past loss was responsible for fully half of the explained variation of 41 percent.

Using the most significant factors shown from these analyses, Keen and Grant (*U171*) developed a regression equation and alinement chart combining past loss, volume per acre, and percent growth reduction to obtain an estimate of future loss in terms of percent of stand killed annually. Data were not available to include the factor of percent of risk trees, which from the California studies was thought to be highly significant.

Another approach to the determination of area hazard was started in 1938 and 1939, when insect survey crews working under Keen's direction in southern Oregon established 139 one-acre plots and took various data on loss and stand conditions. These data were analyzed statistically by Bedard (*U17*), who summarized the results as follows:

> In the analysis of these one-acre plot data, 16 independent variables were correlated with the mean annual insect loss expressed in percent of stand killed, and it was found that the amount of ground covered with brush showed a significant positive correlation with current loss; the amount of ground covered by reproduction multiplied by its average height showed a highly significant positive correlation with current loss; the stand volume per acre showed a highly significant negative correlation; and tree vigor showed a significant negative correlation.
>
> The factor of brush was eliminated and the three remaining factors combined with current loss in a multiple regression which resulted in a highly significant multiple correlation coefficient which showed that about 21 percent of the variability in current loss was explained by these three facors. The factor of reproduction accounted for 43 percent of the explained variation and stand volume for about 35 percent.
>
> In the light of other studies, this suggests that a multiple correlation combining past loss, percent of high risk volume, volume per acre, ground cover, and percent growth reduction would explain a high percentage of the variation in future loss.

Using data from loss and stand cruises already available in the files, Keen (*U153*) in 1939 devised an empirical method for determining area hazard. He recognized 10 factors as possibly having some influence on hazard: (1) life zone, (2) elevation, (3) temperature, (4) past losses, (5) growth rate, (6) forest type, (7) site quality, (8) stand volume, (9) stand structure, and (10) fire history. Five of these (numbers 2, 4, 6, 7, and 8) were combined on an equal basis by a system of transparent map overlays to arrive at an estimate of future hazard. It was found that the final hazard map derived in this manner required some modification by personal judgment of an entomologist familiar with the area in question.

When a new stand cruise was made of some 112 320-acre check plots in Oregon and Washington in 1942, the green stand was "risk rated" by the California system. By 1947, 92 of these plots remained uncut and had 5 years of annual loss recorded. This enabled Robert A. Merriam, working under Keen's guidance in the spring of 1952 (*U172*), to make new statistical analyses of the factors most indicative of hazard. The most significant multiple regression equation for determining expected future ponderosa pine loss in terms of average percent of stand killed per year was one that integrated the factors of (1) volume of ponderosa pine per acre in M board feet, (2) number of Risk 4 trees per 100 acres, (3) past loss in number of pine snags per 100 acres, and (4) percent of normal growth in last 5 years. The multiple regression equation thus determined was $Y=0.71-0.025x_1+0.001x_2+0.002x_3-0.006x_4$. From this formula an alinement chart was prepared. The standard error of estimate was calculated to be 0.27 percent of the stand. This equation represents the best integration of hazard factors obtained from any of the hazard studies so far conducted.

Special Environmental Hazards

Disturbances of environmental conditions, either natural or man-made, may at times greatly increase the hazards of western pine beetle epidemics within an area. Most important of these are the slash created by logging and clearing, windfalls, and forest fires.

Slash Areas

Under certain circumstances slash creates conditions favorable to the buildup of western pine beetle populations. These conditions, however, are so sporadic that generalizations regarding the relation of slash to epidemics of the wesern pine beetle are often contradictory. The matter has developed much controversy among entomologists and foresters.

One of the first forest entomologists to stress the entomological danger of slash was Ralph Hopping (*50*, *53*) who held the opinion that ponderosa pine slash should be regarded as a potential source of western pine beetle epidemics, particularly when slash included the larger parts of the main bole providing bark areas suitable for brood development. This was concurred in by Swaine (*131*) and represented the viewpoint of the Canadian forest entomologists.

A series of studies was made in California and Oregon from 1921 to 1934 by the western laboratories of the Division of Forest Insect Investigations to determine whether the western pine beetle successfully bred in slash left from logging and right-of-way cuttings, and how often and under what conditions epidemics occurred as a result of these operations.

Person (*U234*) studied the success of western pine beetle broods in slash material left on 11 logging areas and 2 right-of-way clearings in Oregon and California. He found that the ratio of beetles emerging to parent beetles attacking was far less than in infested standing trees. The averages from 1,425 pieces of slash examined showed 15.6

beetles attacking to 19.0 beetles emerging per square foot of bark. This represented such a small increase in progeny that practically no buildup of beetle population in the area was possible. In the areas studied, no serious western pine beetle epidemics occurred. Person attributed poor brood development to the rapid drying out of the slash material. As a result of these studies, he suggested scattering slash so that it would be well exposed to the sun. If this were done, the slash would be much less likely to develop beetle populations than if it were piled and the larger pieces shaded.

The slash left from right-of-way clearings where the trees are not promptly utilized (where logs are usually pulled to one side and frequently left under shade) was considered to create conditions much more favorable to an increase in beetle population than logging slash (in which the bulk of the logs are promptly removed from the woods). Patterson (*106*) made a study of highway clearing in southern Oregon from 1920 to 1924, and found that the western pine beetle was attracted to the down logs in numbers, but that brood development was poor. "The increase of beetles developing in the slash was only 64 percent of the beetles making the attack (in reality a decrease in population of 36 percent), whereas there was an increase in adjacent standing timber of 135 percent."

Patterson studied the course of the infestation in zones on either side of the right-of-way for 2 years before and 3 years after the timber cutting, and concluded that:

> Bark beetles from the surrounding standing timber are attracted to the slash at the time of attack, and a temporary concentration of infestation occurs in its immediate vicinity. Normal distribution of the infestation is resumed within a year.
>
> The concentration just mentioned and the breeding of beetles in line slash do not increase or greatly influence infestations in the surrounding forests. The cycle of an infestation continues regardless of the slash.

After studying the effectiveness of different ponderosa pine "line" slash-disposal methods, Person (*U239*) concluded that "the potential from beetles attacking standing trees is so much greater than that from beetles attacking slash, that any effect on the total infestation would be toward a decrease rather than an increase" in western pine beetle population. He recommended that trees along right-of-ways be felled and limbed, or felled, limbed, and the brush burned over the trunks to make them even less attractive to the western pine beetle.

Beal (*U4*, *U5*, *U7*, *U8*, *U9*) studied the entomological aspects of slash on large logging operations in southern Oregon. His results for the most part confirmed those of Person and Patterson. He found that the western pine beetle was not able to reproduce itself rapidly in logs and slash resulting from logging operations. While slash was attractive to the beetles, it usually failed to produce successful broods. Beal (*U9*) states: "The inability of this insect to increase rapidly in slash and felled logs should eliminate it from serious consideration as a menace in ponderosa pine slash areas." He gave

special attention to the distances from which beetles may be attracted to down logs and concluded that this influence did not extend more than one-half to three-quarters of a mile in the surrounding timber. He found that logging slash had little effect upon the course of the infestation in adjacent unlogged areas.

In order to clear up the various issues over the entomological aspects of slash disposal, the Division of Forest Insects published a circular in 1927 (*23*) summarizing previous publications and the investigative work that had been done up to 1927. This publication points out the following conditions concerning the western pine beetle in ponderosa pine:

> Usually the first effect of slash was to increase the infestation in standing trees in the vicinity. In every case, however, this increase occurred simultaneously with the attack in the slash, instead of following the emergence of beetles breeding in the slash.
>
> Since the western pine beetle breds only in slash matrial more than 6 inches in diameter, such as cull logs and butts, the present methods of slash disposal can be of little avail in reducing the number of beetles. Neither can the very strong attractive influence of the slash be avoided. The best way, therefore, to avoid injury to neighboring standing trees is to supply continuously a quantity of logs to absorb the beetles and if necessary to reduce through artificial control the total population of beetles on the area.

This same bulletin recognizes that slash is potentially dangerous as a breeding place for aggressive engraver beetle infestations.

> When they (*I. emarginatus, I. oregoni, and I. confusus*) become sufficiently numerous, if there is a shortage of slash, they may kill young trees and the tops and limbs of larger trees. This damage is very sporadic and usually follows the interruption of logging operations in the summer months.

Although there are no reports or records dealing specifically with the relation of western pine beetle infestations to outbreaks of engraver beetles originating in slash, information from surveys shows heavy infestations of the western pine beetle following widespread top-killing of large trees by engravers. In reviewing the records of the California five-spined engraver, Miller (*U201*) stated:

> The more serious of these epidemics (of *I. confusus*) have been in association with or followed by *D. brevicomis* which bred up in the green boles of topkilled trees and carried on the momentum of the epidemic for several years after *Ips* subsided.

Underlying this hazard of western pine beetle epidemic following engraver beetle outbreaks is the susceptibility of top-killed trees. This is shown by studies of Keen (*U127*), who found on the Ashland areas that 26.6 percent of the trees top-killed by the California five-spined engraver were attacked by the western pine beetle within 1 year after top-killing; and by Person (*U238*), who found on the Cascadel area that 43 percent of the top-killed trees were attacked within 2 years after top-killing.

Engraver beetle outbreaks resulting from slash seem to be connected with climatic and seasonal conditions occurring at the time

the slash is cut or soon after. Interrupted cuttings appear to be specially hazardous during drought periods. Slash created in the spring or early summer is more productive of engraver beetle outbreaks in standing trees than that created in the late summer and fall. This was best shown by Buckhorn (*U37*, *U38*, *U39*) in studies of logging areas in eastern Oregon.

Struble (*U307*, *U311*) brought out a number of inconsistencies in the behavior of engraver beetle infestations in and around slash concentrations. In some of the areas the California five-spined engraver bred large populations in fresh green slash during the spring and early summer, then attacked living trees in adjacent stands during the late summer and fall. In other areas, however, where engraver beetles produced large populations in green slash, no subsequent attacks occurred in standing trees anywhere near the slash area.

As a general rule, slash concentrations that produce heavy engraver beetle populations rarely serve as a breeding ground for the western pine beetle. Slash concentrations, therefore, do not lead to western pine beetle outbreaks unless engraver beetles top-kill a large number of trees of large diameter. Under such conditions, an increase in losses caused by western pine beetle populations can be expected.

Windfall Areas

Windfalls may be regarded as a form of slash created by natural forces. In areas of heavy winter windfall and moist soil, many trees are pushed over leaving part of the root system attached in the soil. Such trees may continue to live in this prostrate weakened condition for several years, maintaining moisture in the inner bark so that conditions are favorable for the attack and brood development of bark beetles. In this important respect, most logs from windfalls differ from those left in logging, where the trees are cut off at the stump and a rapid change takes place in moisture conditions of the main bole. As a general rule, heavy windfall damage has been followed by an increase of western pine beetle infestations in the surrounding timber stands within a season or two.

Windfall damage can be roughly classed according to the amount of down material within the area affected. Some windfalls consist only of scattered trees; other damage results from violent storms that blow down entire masses of trees, sometimes amounting to a relatively high percent of the stand on local areas.

Where mass windfalls have occurred, severe infestations of the western pine beetle have followed. One such epidemic on Mendocino National Forest, Calif., was studied by Miller (*93*). A violent windstorm in January 1921 resulted in the blowdown of the following estimated board-foot volume of timber on about 20,000 acres: ponderosa pine, 15 million; Douglas-fir, 8 million; sugar pine, 2 million.

At the time of the blowdown, western pine beetle infestations in the area had been endemic for a number of years. Developments that followed are described by Miller:

> With the sudden creation of this great volume of down logs it was obviously impossible for this limited bark-beetle infestation

to furnish attacking insects for all of the favorable host material in the spring of 1921. It was necessary first that the beetles increase their numbers. This increase developed rapidly during the first season after the windfall, but it occurred almost entirely in the down logs. The degree of infestation in the standing trees that were killed did not increase materially over that of the two seasons preceding. In the spring of 1922 there was no indication from the number of standing infested trees that a potential bark-beetle outbreak existed in the region of the windfalls.

Suddenly, during June and July of 1922, the western pine beetle began to attack standing trees in unprecedented numbers. Trees were killed in groups of from 50 to 100, whereas in previous seasons such killings occurred only in single trees or in groups rarely exceeding four or five . . . The infestation resulting from the attack of this summer generation of beetles suddenly increased the losses from 25 to more than 200 trees per timbered section.

In the fall of 1922 the attacks of the generation of beetles that was to hibernate showed a very pronounced falling-off in numbers. The large grouping of the attacks disappeared, and the additional loss dropped to less than 30 trees per timbered section. In 1923 the seasonal loss declined to a point even lower than that for 1921, the year preceding the windfall.

Significant features of this epidemic were (1) the absence of engraver beetle outbreaks in ponderosa or sugar pine (although engraver beetles were noted in some of the down logs, they did not appear as a factor in the subsequent killing of standing timber); and (2) the striking absence of any noticeable killing of standing Douglas-fir. This species comprised a high percent of both the windthrown material and the surviving stand, but insects that bred in the windfalls were incapable of starting aggressive outbreaks.

Keen (*U147*) reports a violent windstorm in 1921 that toppled about 6 million board feet of ponderosa and sugar pine in a localized area near Fort Klamath, Oreg. Unlike the Mendocino windfall reported by Miller, this one did not produce spectacular bark beetle outbreaks in surrounding timber. Instead, it was followed by only moderate increases in bark beetle losses during the second and third year after the blowdown.

The most extensive bark beetle epidemics associated with windfalls yet recorded occurred in the pine types of Washington, Oregon, and parts of Idaho and California following a windstorm in April 1931. These are described by Keen (*U147*):

Combining a heavy beetle emergence from the windfalls with conditions of low tree resistance, the year 1932 set a high mark for bark beetle destructiveness in the ponderosa pine stands of Oregon and Washington.

Following the blowdown of April 1931 bark beetles attacked and bred in these down trees during the summer of 1931 and emerged in large numbers in the fall. The first heavy loss in standing timber resulted from these fall attacks, which turned out new broods in the early summer of 1932. New attacks were greatly increased during the summer and fall of 1932, even though beetles

breeding in the windfalls were no longer a factor. So in this case we have an example of an epidemic once started in windfalls increasing for two seasons in strength and virulence instead of coming to a sudden end.

In Klickitat county, Washington, where there was a 25 percent loss of timber due to the wind, there developed an additional 15 percent due to bark beetles. On an area of about 200,000 acres in and adjacent to the Ochoco National Forest in central Oregon windfalls were scattered throughout the forest and were followed by a beetle kill of 10 percent of the remaining stand. On the Metolius area of the Deschutes, the loss of timber due to beetles following the blowdown represented 2 percent of the stand. In fact, spotted throughout the pine region in every place where the windstorm had struck, subsequent losses from bark beetles had occurred. The total loss of prime timber in 1932 is estimated at over a billion board feet.

Weaver (*141*) describes infestation conditions that followed this April 1931 windfall in reserve pine stands on cut-over areas of the Klamath Indian Reservation. During the summer of 1931:

> . . . the top sides of the logs were attacked by the Oregon pine engraver beetle (*Ips oregoni*) and by the pine flat-headed borer (*Melanophila gentilis*) while the under and shaded sides of the logs were attacked by the western pine beetle (*Dendroctonus brevicomis*) and the mountain pine beetle (*Dendroctonus monticolae*). While it was apparent that each windfall supported only a light brood of the western or mountain pine beetles, the windfalls themselves were so numerous that in the aggregate they contained a vast horde of insects.
>
> The unusually heavy precipitation of the winter of 1931–32 was so favorable for tree growth that it was thought the beetles would make no headway in the standing green trees. However, as the summer advanced, large groups of trees in the vicinity of the previous year's windfalls began to fade and die from beetle attacks. Groups of 10 to 15 thrifty, vigorous trees with breast high diameters ranging from 10 to 30 inches, were frequently successfully attacked.

A spectacular outbreak of western pine beetle, reported by Struble (*U305*, *128*) occurred near Bass Lake on Sierra National Forest in 1945. This outbreak followed a mass type of windfall, but was limited to about 500 acres. The storm causing the damage occurred in January 1944. During the season of 1944, the western pine beetle confined its attacks to windthrown trees; then, in the midsummer of 1945, there was a sudden outbreak of the beetles in the surrounding area. Groups of 10 to 30 infested trees were common. The heaviest kill and the most frequent grouping were found within the blowdown area, but some isolated groups occurred as far as 6 miles away. This epidemic was similar to that of other windfalls of the mass type both in its timing after the windfall and in the absence of any noticeable engraver beetle activity in the attacks on standing trees (fig. 44).

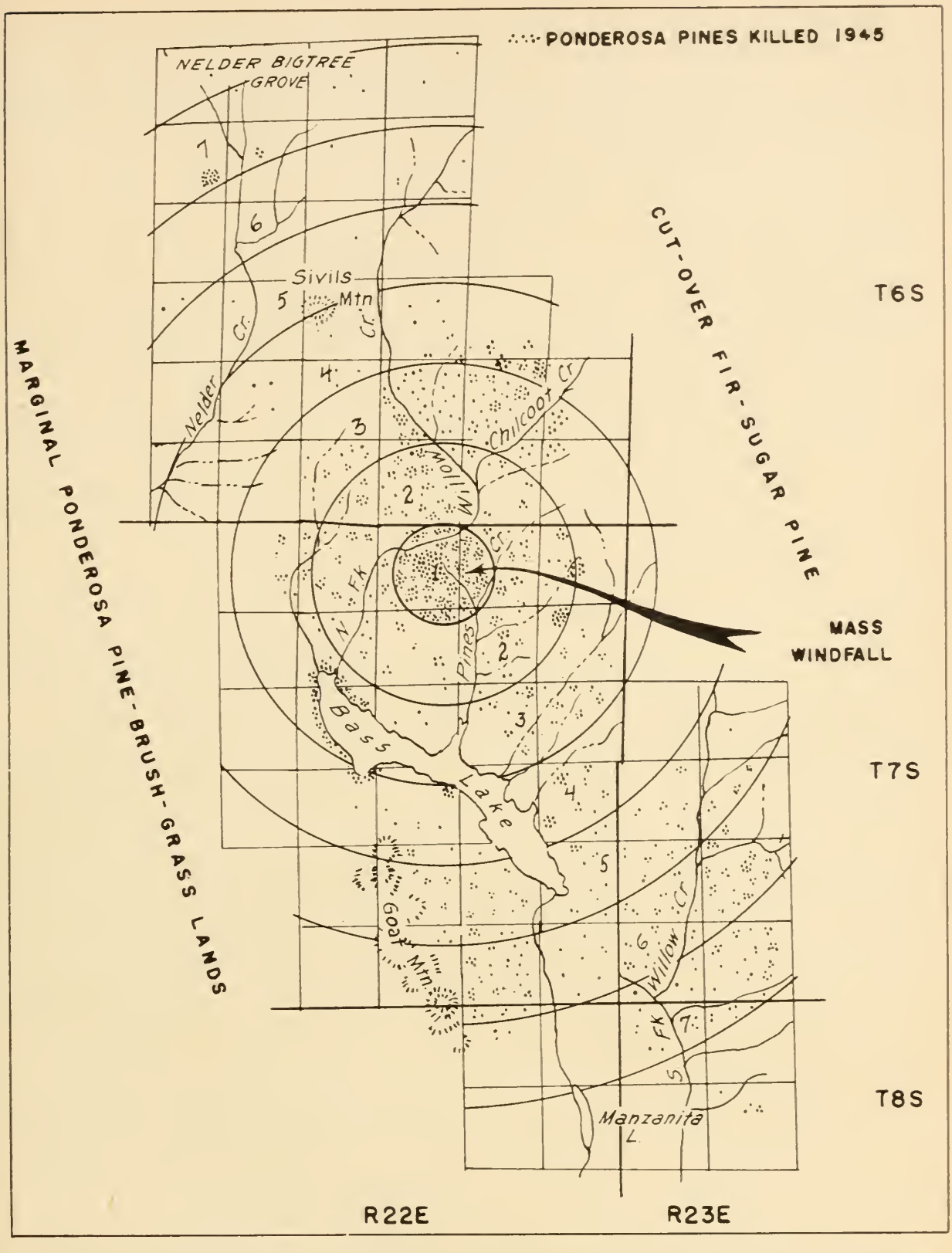

FIGURE 44.—Infestation of the western pine beetle in 1945 resulting from McLeod Flat blowdown of January 1944, Sierra National Forest, Calif.

Effects of the light, scattered type of windfall upon western pine beetle infestations have not been studied, although windfalls have occasionally been referred to in survey reports as the source of certain outbreaks. According to Struble (*U305*):

Almost every year there are localized blowdowns in certain of forested areas. The scattered character of these logs through the woods tends to minimize their importance as breeding places for

bark beetles. The facts, however, are that while separate trees do not breed populations sufficient to cause a virulent type of epidemic, they do increase to a certain extent the number of killed trees within the locality of the windfalls and because of this they too must be regarded as menacing to living timber.

Forest Fires

The evidence of fire scars imbedded in tree rings shows that mature ponderosa pine stands have been subjected to repeated fires throughout their history. Basal sections taken from the edges of scars on fire-scarred trees on more than 100 permanent sample plots scattered throughout eastern Oregon and Washington showed that all plots had experienced repeated fires at intervals of about 15 to 20 years. One stump section showed a record of 25 fires at approximately 18-year intervals back to the year 1481 (*70*). Since fires at irregular intervals are an important phase in the ecology of these stands, they cannot be disregarded among environmental influences affecting the western pine beetle.

History of Investigations

Interest in the effect of fires upon bark beetle infestations developed very soon after the beetle problem became recognized as an important part of forest protection. Hopkins (*44*) regarded fires as both favorable and unfavorable to *Dendroctonus* beetles, depending upon the area and conditions at the time of the fire. A live interest in the relationship of fires to bark beetle infestations in ponderosa pine stands began to develop about 1915, stimulated in large measure by a school of thought that advocated "light burning." Some lumbermen, stockmen, and others who were familiar with conditions in pine stands before the suppression of forest fires became the chief objectors to forest protection. They argued that fires, when not too severe, had a controlling effect upon bark beetles. It was assumed that in some way fires destroyed the bark beetles and thus protected trees from attack.

The issue of light burning was brought into the open by Stewart Edward White (*147*, *148*, *149*), nationally known author, who stated the case for "light" or "surface" burning quite effectively. His position was opposed by Chief Forester Graves (*37*), who replied by stating the viewpoint of the U. S. Forest Service.

Some advocates of light burning carried their ideas into practice. For several years before 1918, a major lumber company burned over a considerable acreage of their holdings in northeastern California with controlled fires. Their primary purpose was to improve ground conditions for early logging, but they also advocated light burning as a measure for protecting mature trees from bark beetle attack. Other less responsible advocates of the theory started fires surreptitiously whenever they considered conditions to be right, either for selfish ends or in the belief that burning would be for the general good of the country.

All of this agitation for light burning ran counter to the efforts of the Forest Service and other forest protection agencies to establish a strong fire exclusion policy in pine stands. Arguments for and against light burning including its entomological aspects became highly controversial and the theory was praised by some and denounced by others without much supporting evidence on either side.

The need for factual information on the effects of fires in ponderosa pine stands and their relation to bark beetle epidemics led to a series of studies and experiments by the Forest Service and the Forest Insect Division extending over the period from 1919 to 1938. Eleven individual burns involving western pine beetle infestations in ponderosa pine type were studied and analyzed. In addition, data were collected on annual bark beetle surveys on 10 other burns.

The study areas were distributed in both eastside and westside pine type from Cleveland National Forest in southern California to Coeur d'Alene National Forest in Idaho. All types of burns from light ground fires to heavy crown fires were represented in the studies. Phases of the investigation included (1) the immediate effect of fire upon the current beetle population, (2) the relative losses caused by fire and beetles within the burns, (3) the relation of fire injury to beetle attack, and (4) the effect of fires in the ecology of ponderosa pine stands.

The burns that have been studied and analyzed (table 9) can be grouped into the following categories:

(1) Controlled burning experiments to test the practicability of light burning and to study the silvicultural and entomological effects—the Snake Lake and Weed Lumber Company burns in California.

(2) Uncontrolled fires causing varying degrees of damage studied to determine the reaction of beetle populations within and around the burns—Chinquapin, Mistletoe, and Siskiyou burns (*U204*, *U217*), Northfork burn (*U196*, *U199*), Aspen Lake burn (*U225*), Sugar Hill burn (*U249*, *U290*), Parker Mountain burn (*U223*), and Tubbs Hill burn (*U254*).

(3) Uncontrolled burns studied both for the immediate effects of the fire and (by extended records covering some 20 years) for the long term effects of fire on western pine beetle environment—the Northfork (*U199*) and South Ice Cave (*U163*) fires.

Direct Control by Fire

One of the arguments advanced in the light burning controversy was that fires are Nature's way of keeping bark beetle infestations in check. White (*148*) suggested that these insects may harbor in duff or other ground cover and be destroyed by surface fires; he also advanced the idea that the heat or smoke from fires either kill the beetles in flight or drive them out of an area. Forest entomologists have shown, however, that the western pine beetle does not harbor or hibernate in duff and spends but a relatively short part of its life in the flight stage. Thus the chances of adult beetles being killed by fires are too small to be of importance.

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TABLE 9.—*Studies of bark beetle conditions following fires in ponderosa pine type*

WESTERN PINE BEETLE INFESTATIONS

Burn	Date and location	Acres	Type of burn and special conditions	Volume of beetle-caused loss following fire compared with loss for year preceding		
				1st year	2d year	3d year
Chinquapin	September 1915, Ashland, Oreg.	220	Hot ground fire with medium crown injury.	+475 percent	Decrease	Increase.
Mistletoe	October 1917, Ashland, Oreg.	800	Mixed ground and crown fire with varying degrees of defoliation.	+1,150 percent	+336 percent	+122 percent.
Siskiyou	August 1918, Ashland, Oreg.	200	do	+1,700 percent	+2,880 percent	+1,210 percent.
Northfork	June 1924, Sierra, N.F.	5, 460	Mixed ground and crown fire with high percent of defoliated trees.	+843 percent	+4,680 percent	+482 percent.
Aspen Lake	July 1926, Klamath Falls, Oreg.	8, 000	Mixed ground and crown fire, defoliated trees salvaged within year after fire.	Slight increase	Normal	Normal.
Sugar Hill	July 1929, Modoc, N.F.	5, 000	Mostly severe crown fire with about half of stand fire-killed; severe cambium injury in surviving trees.	+326 percent	+340 percent	+49 percent.

Parker Mountain.	July 1924, Pinehurst, Oreg.	15,000	Mainly a north slope surface fire; severe crown injury occurred only in reproduction thickets.	Heavy increase 1st year after fire due to mountain pine beetle in sugar pine; slight increase in western pine beetle.		
Tubbs Hill	September 1928, Coeur d'Alene, Idaho.	30	Mixed ground and crown fire with varying degrees of defoliation.	Increased loss immediately following fire due to attraction of *Dendroctonus monticolae*, *Ips*, and *D. valens* to fire-scorched trees; infestation normal by 3d year after fire.		
CONTROLLED BURNING OPERATIONS						
Snake Lake	May 1920, Quincy, Calif.	200	A controlled light burning experiment; burning at night by surface fire.	+1,465 percent	+915	Above normal.
Weed Co. Light Burning Project.	June–October 1920, Bray, Calif.	12,000	Area burned at night in small blocks of not more than 160 acres each.	About 10 percent increase on burned area as compared to unburned areas, 1st and 2d years.		
RECOVERY OF PINE STANDS FROM FIRE INJURY AND BEETLE LOSSES OVER A LONG PERIOD						
South Ice Cave	August 1915, Deschutes, N.F.	10,000	Mixed ground and crown fire with varying degrees of crown injury.	22 years after the fire the green volume per acre was about the same on burned as on unburned areas. Fire destroyed young trees in stand but high percent of older trees survived.		

Another theory is that fires destroy broods of the beetle in infested trees. However, after the beetles become established in trees, both adults and broods are protected from heat by the thick insulation of the outer bark. This explains why records of brood mortality in trees infested at the time of fire are rare.

Additional evidence of the insulating effect of bark is provided by experience on many control projects, showing that western pine beetle broods survive when the bark of treated trees is not thoroughly charred (see Section V). Miller and Patterson (*U204*) reported six infested trees on the Mistletoe Burn exposed to considerable heat at the time of the fire, but in only one case was there any evidence of brood mortality caused by the fire. In the published summary Miller and Patterson (*99*) stated: "Fires which are not severe enough to burn the bark from infested trees are of little value in controlling bark-beetle infestations. Fires of moderate severity do not kill bark-beetle broods in infested trees at the time of the fire."

Attraction of Bark Beetles to Burned Areas

Bark beetle populations usually concentrate in fire-injured trees surviving a fire, indicating that these trees are especially attractive to the beetles. The odors from smoke produced by burning resins and pine foliage have been suspected as a possible attractive influence, but a review of data from fire studies indicates that the western pine beetle is not attracted to burns until long after the odors of the fire have disappeared. On the Mistletoe, Northfork, and Tubbs Hill burns, it was noted that the main force of the western pine beetle attack occurred during the season after the fire.

Miller (*U196*) reports an experiment in which ponderosa pines were scorched by controlled burning in April to produce varying degrees of fire injury. None of these trees were attacked until late September, after any odors caused by the immediate effects of the fire had disappeared. The western pine beetle then attacked two of the most heavily defoliated trees, neither of which had made any perceptible radial growth during the May-to-September period following the fire.

The evidence is fairly conclusive that the western pine beetle is not drawn to burns by odors from any immediate products of the fire, but rather that it concentrates in burns because of some attractive influence in the tree that sets in some time after the fire.

It has been found, however, that mountain pine and red turpentine beetles may be attracted to fire-injured trees very soon after a fire. Show (*U291*), reporting on the Snake Lake burn, stated that "the mountain pine beetle attacked fire-scorched trees soon after the area was burned in May." On the Tubbs Hill burn, Rust (*U254*) found that a large number of mountain pine beetles were attracted to the burn within 6 to 10 days after the fire. The time interval in these cases indicates that the odors from the fire or from its immediate after effects could have been an important factor in drawing these insects to the burn.

It is well established that other species of cambium-feeding and wood-boring insects are attracted to burns almost immediately, although these secondary species have been treated only incidentally in the recorded burn studies. Certain buprestids, especially *Melan-*

ophila consputa Lec. and *M. acuminata* DeG., come to burns (*85*) and attack fire-killed trees in great numbers even while the fire is still in progress. At times these insects become an extreme annoyance to the fire fighters by biting them on the neck and arms. These species of beetles appear to be attracted over long distances by the odor of smoke. They come to forest fires as well as to other burning material, and are also greatly stimulated by heat.

All of the burn studies agree on one point: The western pine beetle is not attracted to trees that have been immediately fire-killed by the burning of all foliage, charring of the bark, and killing of the entire phloem area. The beetle selects trees that have survived the fire with enough green phloem and live buds to permit new needle growth after recovery from the first shock of the fire. The studies also agree that there is a direct relation between the amount of crown defoliation from fire and the selection by the western pine beetle of these surviving trees.

Fire-Defoliated Trees

The relation of crown injury to beetle attack was first studied on the Mistletoe burn. Miller and Patterson (*99*) made an inventory of surviving trees according to the amount of crown injury soon after the fire, and annual records were maintained for the next 3 years showing mortality of fire-injured trees.

	Trees on burns			
Degree of injury:	*Number*	*Dead from effects of fire (percent)*	*Attacked and killed by beetles (percent)*	*Surviving 3 years after fire (percent)*
I. Uninjured by fire	1,577	--------	3.1	96.9
II. Light injury, only lower limbs scorched	573	--------	16.6	83.4
III. Medium injury, more than half of crown scorched	113	--------	92.0	8.0
IV. Heavy injury, all of crown scorched	57	23	67.0	10.0
V. Fire-killed at time of fire	80	100	--------	--------

This classification of trees on burns according to degree of fire injury pointed to scorching of the crowns, or defoliation, as a dominant factor in the relation between fire injury and subsequent attack by bark beetles. On the Northfork burn in 1924, a more critical classification of crown injury according to percent of defoliation was used on three plots of 100 trees each.

	Trees on burns			
Class of injury:	*Number*	*Killed by fire (percent)*	*Killed by beetles (percent)*	*Surviving 4 years after fire (percent)*
I. No injury visible	27	--------	--------	100
II. Less than 25% defoliated	61	--------	--------	100
III. 25 to 50% defoliated	32	--------	13	87
IV. 50 to 75% defoliated	45	--------	42	58
V. 75 to 100% defoliated	125	--------	87	13
VI. 100% defoliated, bark-charred, cambium-injured	10	100	--------	--------

The board-foot volume in each fire injury class and the subsequent insect loss in each as estimated on the basis of sample strips for the entire Northfork burn are shown in figure 45.

The same classification by percent of crown defoliation was later used in studies on the Sugar Hill burn by Salman and Wohletz (*U290*) and on the Tubbs Hill burn by Rust (*U254*). Although the percent of mortality in these studies was considerably lighter than on the Mistletoe and Northfork burn, the same relationship was shown between percent of defoliation and bark beetle attack.

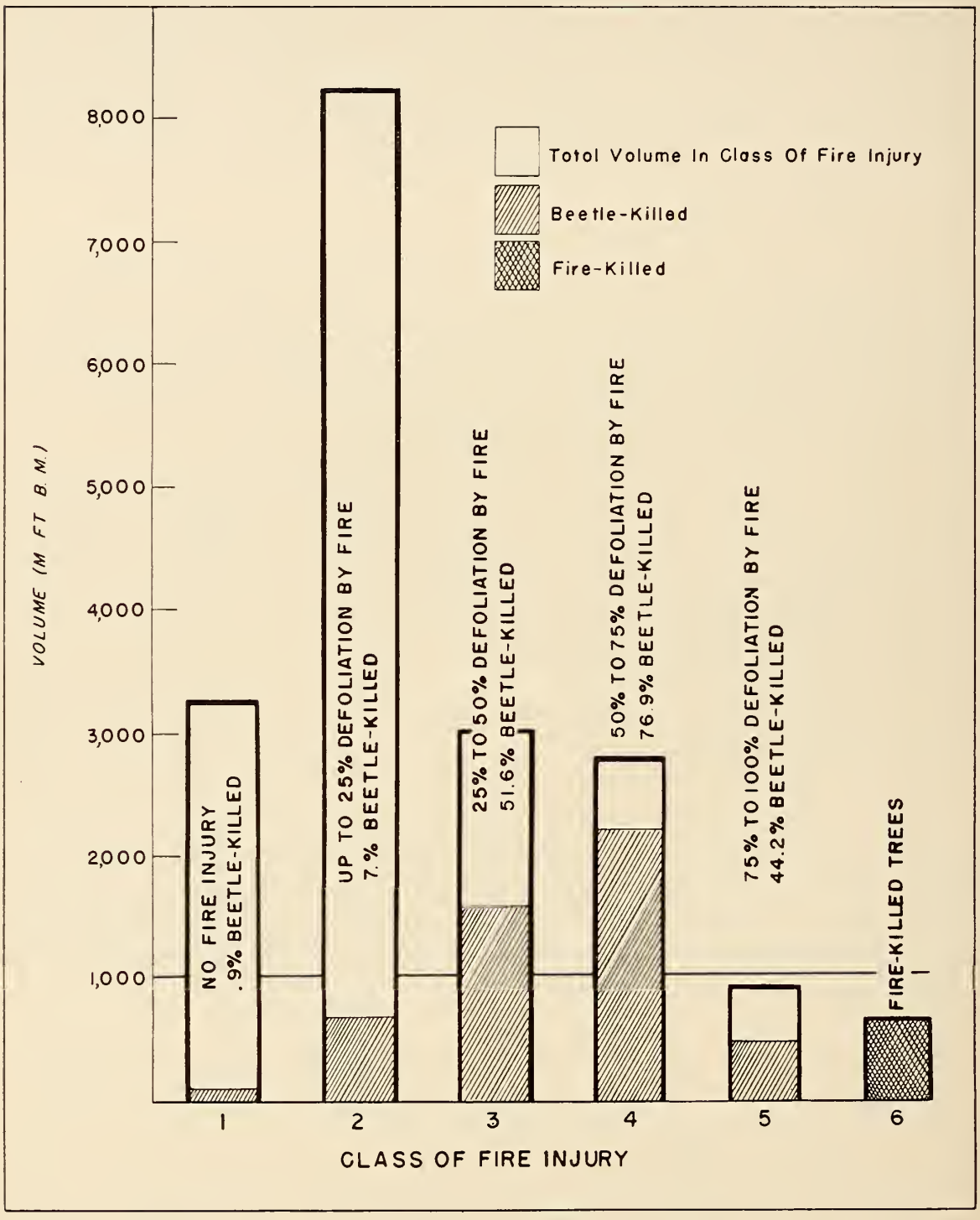


FIGURE 45.—Mortality of ponderosa pine from fire and bark beetles, Northfork burn, Sierra National Forest, Calif. Total volume in each class of fire injury and percent killed by beetles within 3 years after fire of June 21–24, 1924.

Percent of defoliation by fire:	Trees killed by bark beetles: Sugar Hill burn—plot of 148 trees (percent)	Trees killed by bark beetles: Tubbs Hill burn—1,053 trees in burn (percent)
Less than 25	9. 0	14. 5
25 to 50	7. 0	14. 1
50 to 75	23. 3	18. 7
75 to 100	47. 7	44. 6

According to data from the four burns, percent of defoliation is a fairly reliable index to the expectancy of beetle-caused loss in trees surviving fire in the ponderosa pine type. Crown injury by defoliation is perhaps the most easily appraised of any of the effects of fire, and it can readily be applied in surveys of burns for salvage operations.

Cambium-Injured Trees

On the Mistletoe and Northfork burns, attempts to connect visible basal fire scars with susceptibility to bark beetle attack yielded only negative results. Miller (*U199*) reported:

> While it was noted that flathead borers often attacked around the edges of these scars, the records did not indicate any apparent relations between this type of injury and bark beetle attack. It is altogether possible that a considerable amount of cambium injury (due to overheating) was overlooked in this study since the general run of basal injury in this fire did not burn the outer bark sufficiently to expose the cambium.

On the Sugar Hill fire, Salman and Wohletz (*U290*) examined trees for concealed scars in the cambium. They found that neither enlargement of former basal scars by the current fire nor cambium injury in trees that were not defoliated added to the susceptibility of the trees to bark beetle attack. However, it was reported that: "The susceptibility of trees suffering from cambium injury in addition to foliage injury is markedly greater than that of trees suffering from foliage injury alone."

Salman (*118*) made a comparison of tree susceptibility in relation to cambium injury by fire.

Percent of defoliation by fire:	Trees killed by bark beetles: Cambium injury slight (percent)	Trees killed by bark beetles: Cambium injury moderate to heavy (percent)
0 to 25	8. 7	10. 0
25 to 50	3. 6	13. 3
50 to 75	18. 2	37. 5
75 to 100	19. 2	72. 2

On the Tubbs Hill burn, Rust (*U254*) noted that cooking of the cambium around the root collar was an important factor:

> Increased injury to the root collar caused from burning of the extra accumulation of duff on the uphill side of many of the larger pines that escaped severe crown injury was apparent. This severe root collar injury was found to be a deciding factor in the selection of many fire-injured trees by bark beetles.

Studies have shown that the susceptibility of ponderosa pine to beetle attack varies directly with the amount of defoliation caused by fire. This relationship is not greatly changed when cambium injury is also present, except that heavily defoliated trees become still more susceptible if they have moderate to heavy cambium injury. In the lightly defoliated trees, this difference is much less apparent (*118*).

Growth Suppression in Fire-Injured Trees

Forest entomologists have shown definitely that suppression of growth rate resulting from defoliation is the dominant factor relating fire injury and beetle attack during the first few years after a fire. During the first 4 years after the Northfork burn, basal radial growth was measured on all surviving trees on three sample plots. Miller (*U196*) reported that growth was greatly suppressed in the more heavily defoliated trees. In many trees no rings were formed during the first 2 years after the fire:

Percent of defoliation by fire:	*Trees that failed to form growth rings 1925–26 (percent)*	*Trees killed by bark beetles 1925–28 (percent)*
No visible injury	----------	----------
0 to 25	----------	----------
25 to 50	3. 1	13. 0
50 to 75	15. 1	42. 0
75 to 100	83. 2	87. 0

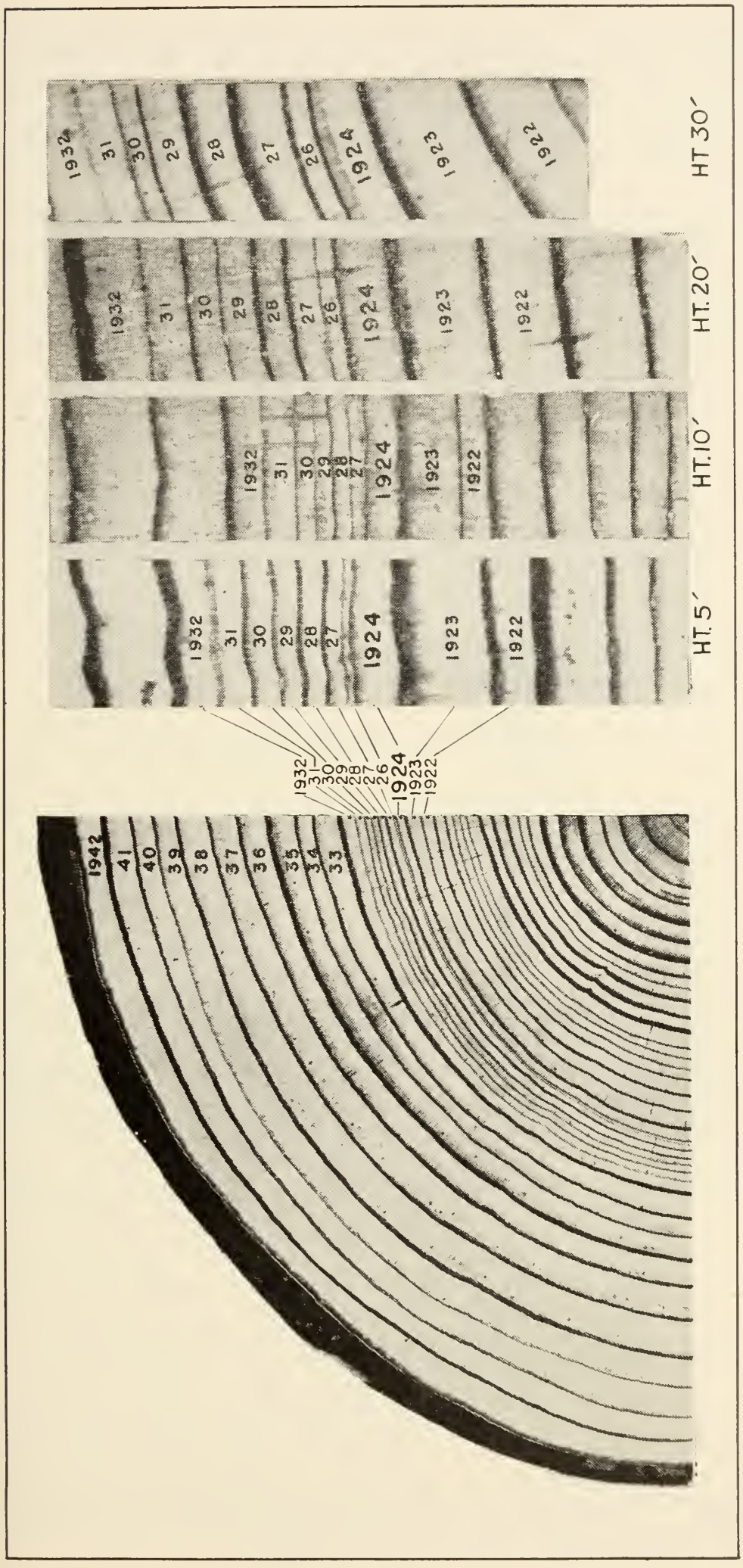
This comparison is based entirely on radial growth at the base of the tree. Practically all trees that failed to show growth rings in 1925 and 1926 put out new needles, and some crown growth was apparent in all trees until they were killed by beetles.

There was some question whether surviving Northfork trees that failed to put on basal radial growth during the first 2 years after the fire formed any radial growth in the upper bole during these years. In 1942 Miller (*U199*) felled two such trees and measured the radial growth at each 10-foot interval up the trunks. He found that:

> There is no significant difference in growth behavior between the base and tops. Missing rings, suppression and recovery of growth rate occurred in the same years at all heights, but suppression of the rings at the base was more pronounced than at the top.

The effect of fire injury on radial growth of one of these trees is shown in figure 46. This tree was a dominant in a group of small pole-sized trees on an area of relatively light burn. More than 75 percent of the needles had been burned off (fire injury Class V). The tree grew new needles in 1925, and continued to grow until it was cut down in September 1942. Growth suppression during the period 1924–32 was marked, resulting from both fire injury and a series of dry seasons.

The enlargements in figure 46 show that no annual ring was formed at any height in 1925, the year following the fire. The 1926 ring is barely perceptible in the lower bole but becomes well



SECTION 20ft. ABOVE BASE OF TREE NO.182 SHOWING GROWTH SUPPRESSION FOLLOWING FIRE OF JUNE 21-24, 1924

ENLARGEMENT OF CORES TO SHOW GROWTH SUPPRESSION AT DIFFERENT HEIGHTS DURING PERIOD 1924–1932

FIGURE 46.—Effect of fire injury on radial growth of ponderosa pine, Northfork burn, Sierra National Forest, Calif., 1924.

marked at 20 and 30 foot heights. The 1927 ring is well formed at all heights on the bole. After 1927 there was a gradual recovery of growth up to the 1933 season, then a 10-year period of greatly accelerated growth. The sudden growth release, 8 years after the fire, can be attributed to final recovery from the effects of fire injury and to release from competing pines and vegetation killed in the fire.

In a light burn area, 75 trees were surviving at the end of 1928. A comparison of average growth rate for each class of crown injury in this area (fig. 47) showed that Class V trees made little or no recovery during the two growing seasons after the fire, whereas the less heavily defoliated classes started recovery after 1 or 2

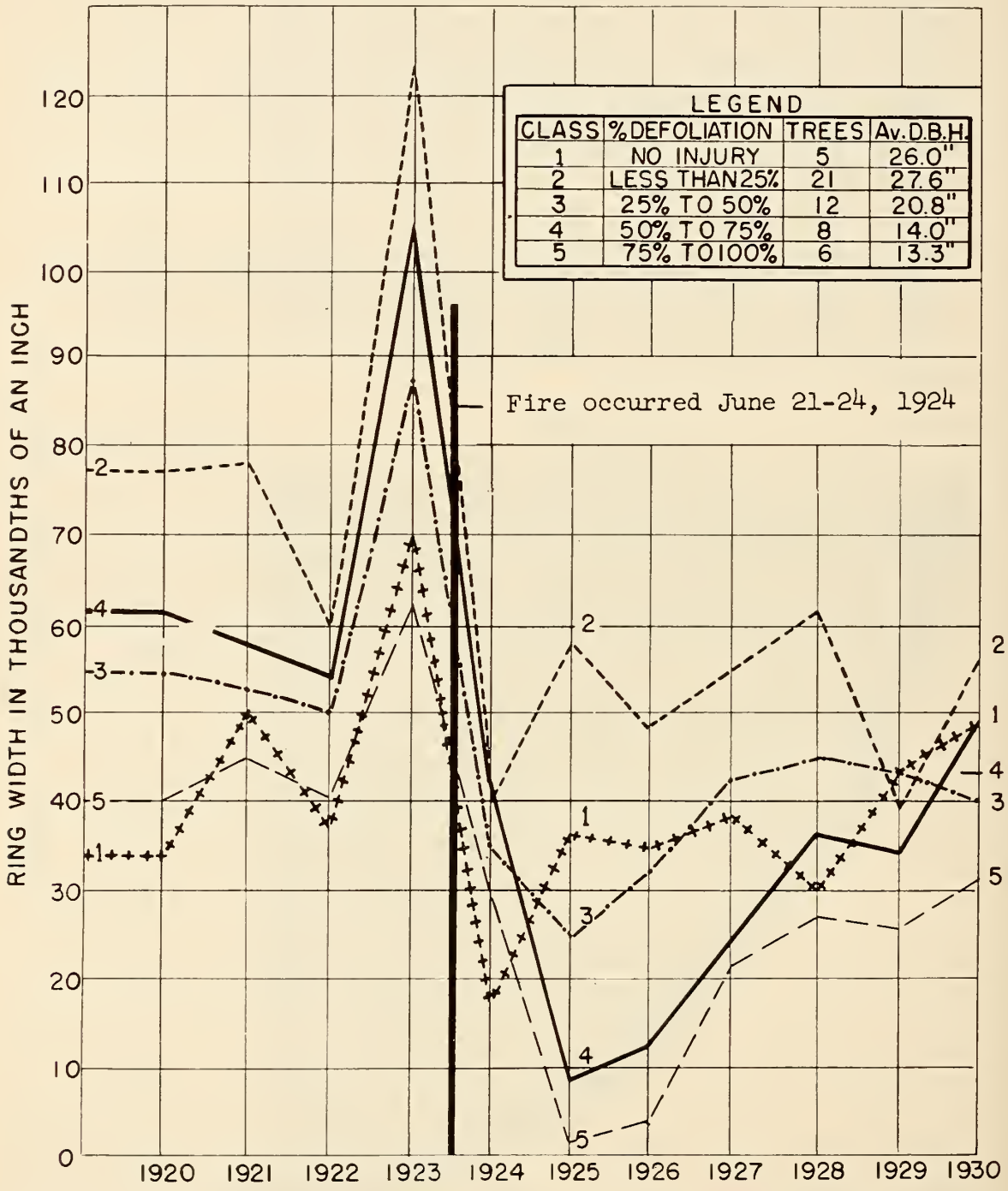


FIGURE 47.—Average annual growth (basal radial increment) by class of fire injury in ponderosa pines surviving on light burn area. Plot 2 (Pine Flat), Northfork Burn Study, Sierra National Forest, Calif.

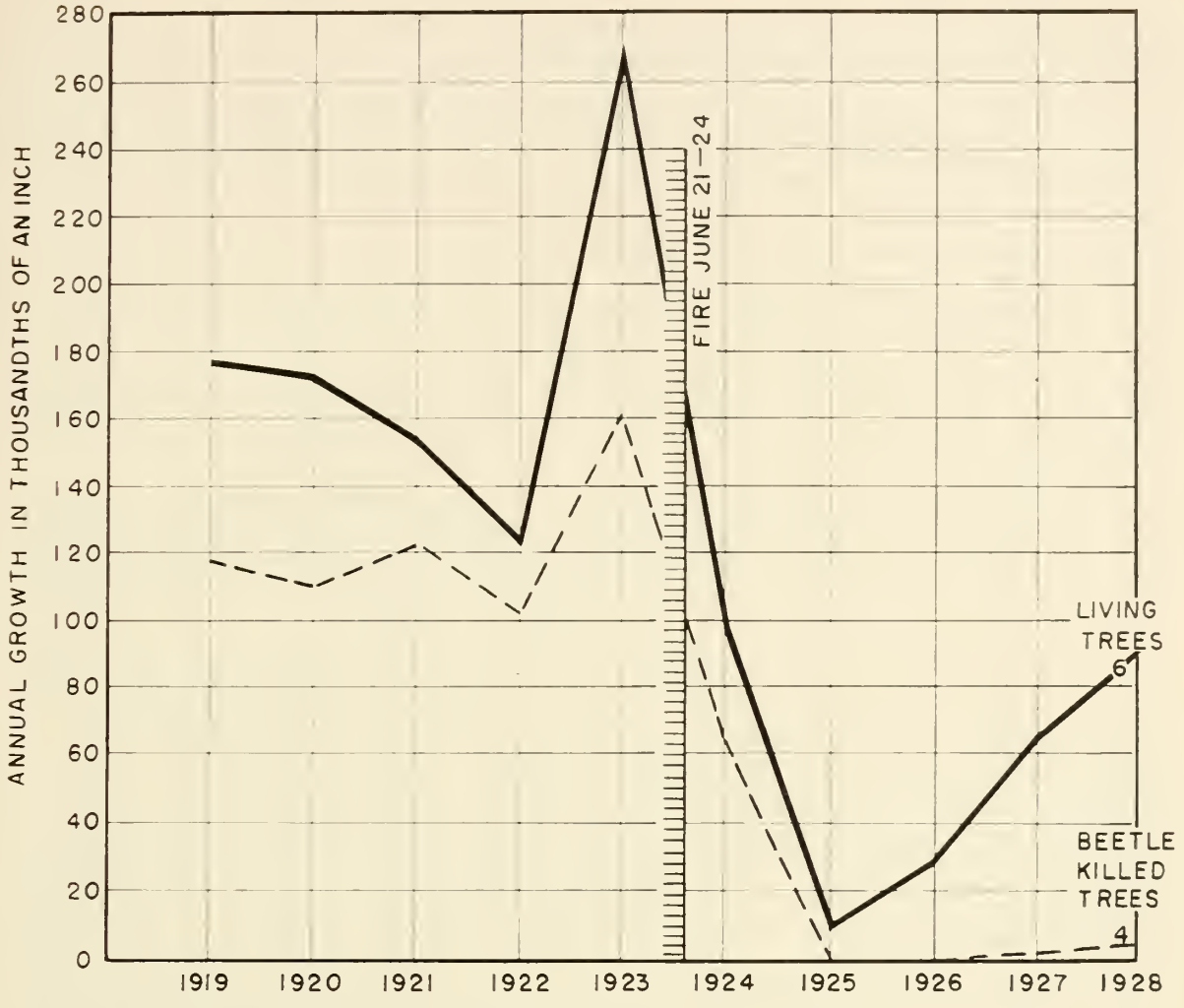


FIGURE 48.—Comparison of average growth (basal radial increment) of surviving and beetle-killed pines on heavy burn, preceding and following fire. Plot 1 (Inspector Trail), Northfork Burn Study.

years. All surviving trees, however, made some recovery in growth the third season after the fire.

In another area representing the heaviest type of burn, only 10 out of 100 trees survived through the season of 1927. In 1928, 4 of these 10 survivors were killed. A comparison of the growth rates of the four beetle-killed and six surviving trees is shown in figure 48. The surviving trees (five in Class IV; one in Class V) started growth recovery in 1925. But the beetle-killed trees, which were a slower growing group before the fire, made barely visible growth up to the time they were attacked in 1928. All six survivors were still living and making vigorous growth in 1943.

Growth Recovery After Fire

Keen studied the long-term effects of fire injury upon the growth rate of ponderosa pines on the 1915 South Ice Cave burn in eastern Oregon (*U163*). Immediately after the fire, three plots of 100 trees each were selected on areas representing light, medium, and heavy types of burns. On each of the plots the trees were classified, described, and marked according to the degree of fire injury to the crowns. In 1938, basal cores from the surviving trees on the plots

were collected and measured. Summarizing the effects of fire injury upon subsequent growth, Keen stated:

1. On the average there was no noticeable difference in the effect of the fire according to the side of the tree (on which the heaviest injury occurred).
2. Growth of small trees was affected slightly more than that of larger trees.
3. Slow-growing trees suffered more than fast-growing trees.
4. Trees less than 50 percent defoliated recovered their normal growth within three years, while trees more than 80 percent defoliated took about nine years to recover normal growth, if they survived.
5. With an increase in percent of crown defoliated, there was a corresponding increase in the number of trees showing missing rings. One living tree was found which had made no ring growth in the lower bole in the 22 years since the fire.
6. Reduction in growth rates in the 22-year period following the fire increased slightly with the intensity of the burn, except that slightly burned areas showed somewhat less reduction in growth than normal unburned areas.

A graph comparing average growth rates before and after the Ice Cave fire in each class of fire injury is shown in figure 49.

In a supplementary report on the Northfork burn based on data from 52 surviving trees 19 years after the fire, Miller (*U199*) said that the trees which had lost 75 to 100 percent of their foliage were the slowest to recover. Within 5 years, however, there was a general

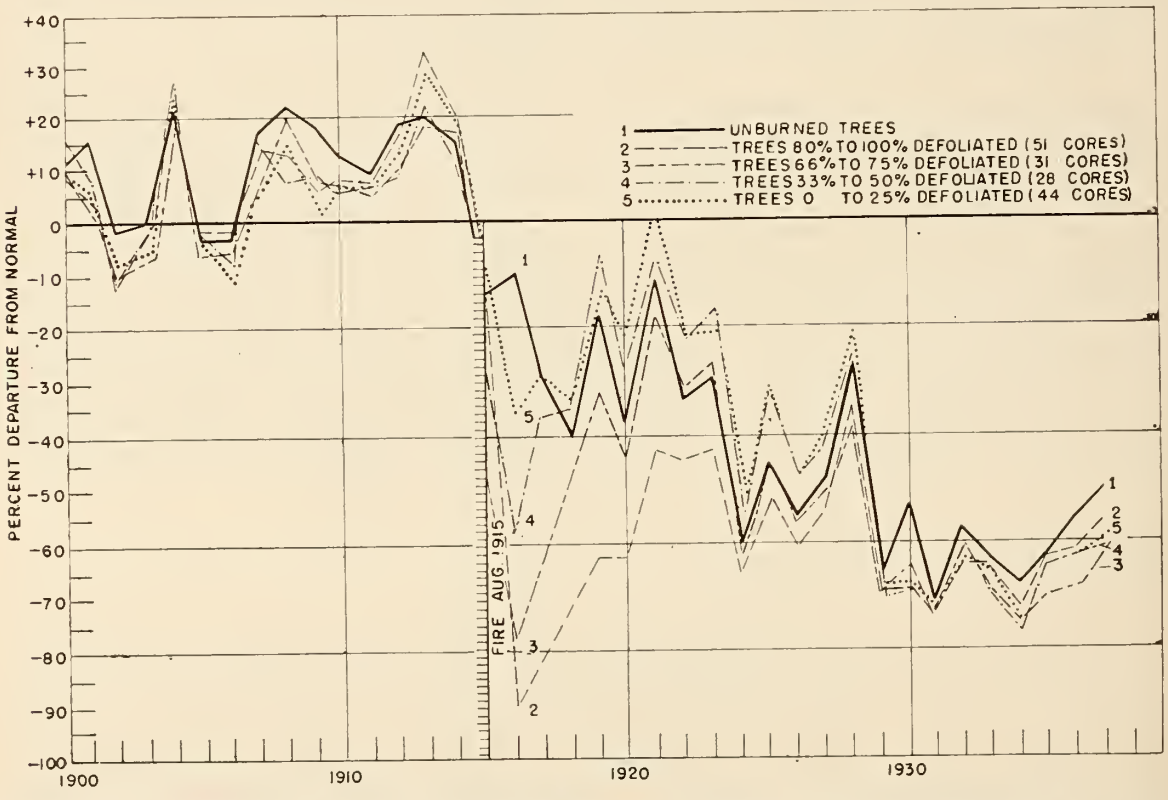


FIGURE 49.—Effect of fire on average growth (basal radial increment) according to degree of fire injury. South Ice Cave Fire, August 1915, Deschutes National Forest, Oreg.

tendency for trees in all classes of fire injury to level off to their prefire growth rates. After this recovery, some surviving trees made phenomenal growth because of release from competition from adjoining trees (compare fig. 46). This recovery in radial growth was accompanied by vigorous growth in the crowns as represented by heavy needle complements, long internodes, and a lush dark green foliage.

Evidence from the growth studies of fire-injured trees points clearly to the conclusion that susceptibility to western pine beetle attack is associated with suppression of growth resulting from crown injury and defoliation, a conclusion supported by the history of western pine beetle infestations occurring in burns after the suppression of growth has set in. The fact that a few heavily defoliated trees sometimes escape attack can be explained by such factors as climatic influence, the chance distribution of beetle populations, or the inherent vigor of certain trees to overcome the effects of fire injury and to resist beetle attack.

Brood Development in Fire-Injured Trees

Studies on three burns show that the success of brood development is related directly to the causes of epidemics that originate in burns. If high brood mortality occurs in fire-injured trees, then epidemic populations cannot be expected regardless of the high concentrations of attack. However, if the brood development is successful and large populations emerge within the burn, the beetles may spread to adjacent timber.

Miller and Patterson (*99*) reported on the Mistletoe burn:

> During the season of 1918 it was found that many broods of the western pine beetle in fire-scorched trees were dying in the early larval stages. In trees where this high mortality occurred it was noted that an extremely moist condition of the inner bark was prevalent. . . . Much of the moisture in the sapwood and cambium condensed in the inner bark, resulting in conditions highly unfavorable to the young larvae of the western pine beetle. The term used by cruisers to designate this condition is 'sour sap.'

Miller and Patterson used a comparison of the number of beetles emerging and the number of parent beetles attacking on the same bark areas to determine brood success in fire-injured trees. Populations were estimated by counting entrance and emergence holes in 272 square feet of bark collected from 28 representative trees on the Mistletoe burn. Similar counts were also made from 341 square feet of bark from 76 beetle-killed trees on adjacent unburned areas.

Item:	*Fire-injured trees*	*Normal trees*
Square feet of bark	272	341
Entrance holes	1, 372	2, 048
Beetles attacking [1]	3, 553	5, 294
Beetles emerging [2]	3, 277	22, 807
Percent of beetle increase (emergence over attack)	----------	318
Percent of beetle decrease	7. 7	----------

[1] Entrance holes x 2.59.

[2] Actual number of emergence holes.

Brood success on the Northfork burn varied somewhat according to the class of fire injury. Twenty trees were selected in each of five classes of fire-injured trees recognized on this burn, and from each tree a 2-foot square piece of bark was collected at each 10-foot height. Some increase of beetles was found in all classes except Class III (25 to 50 percent of crown defoliated), which showed a brood decrease of 63 percent. No consistent trends could be recognized in the other classes. According to Miller (*U196*):

> This would indicate that the beetles built up their number in the more severely injured trees which were attacked the first season after the fire; and that the partially defoliated trees in classes III and IV, which composed the bulk of the attack the second season after the fire, were unfavorable to brood development. The high mortality in trees of these classes may account for the decline of the infestation in 1926.

The amount of bark material on which these averages were based is much too limited for reliable population statistics, and the results cannot be considered conclusive.

> A considerable amount of bark containing overwintering broods of the western pine beetle was taken from fire-scorched trees on the burn in the spring of 1930 and placed in rearing cans for securing reliable data on emergence. An average square foot emergence of 274 beetles was secured from this material showing an average increase of 1,091 percent over beetles attacking, assuming the number of parent beetles per attack equalled two. The emergence per square foot of bark surface for this region secured from a large amount of infested bark surface was found to have a range of 109 to 512, with a general average of 307. The average secured from infested bark from the burn compared very favorably with the average secured from isolated trees over a number of years.

Of the three burns where some effort was made to determine the success of broods in fire-injured trees, two showed conditions unfavorable to brood development while development on the third was highly successful. Obviously the conditions favorable to brood development in fire-injured trees are highly variable in different burns.

Overall Effect of Burns Upon Populations

Although western pine beetles do not always multiply successfully in fire-injured trees, beetle populations in and around burns may be either favorably or unfavorably affected over a period of years by fire-caused ecological disturbances. As a rule, western pine beetles have concentrated in the surviving trees on burned areas in such force within a year or two after the fire that it can only be assumed that the beetles came in from outside areas. Records of loss maintained before and after the Mistletoe, Siskiyou, and Northfork burns indicate an increase of beetle populations and timber loss as a result of the fires. The increase in volume of loss over the year preceding the burns is shown as follows:

Burn:	Acres (percent)	Increase in loss after fire: 1st year (percent)	2d year (percent)	3d year (percent)
Mistletoe	800	1, 150	336	122
Siskiyou	200	1, 700	2, 880	1, 210
Northfork	5, 460	843	4, 680	482

As a result of concentrations of beetle population, all three areas show tremendous increases of infestation during the first and second seasons after the fire and a substantial increase in the third year.

Considered representative of the behavior of infestations that follow larger fires in the westside ponderosa pine type, the infestation on the Northfork burn reached its peak the second year after the fire, then made a precipitous drop. But even during the third year, losses were still more than 4½ times as great as for the year preceding the fire. Loss records indicated that after the third year the infestation dropped below the prefire status and remained in this low endemic state over a long period.

Other burns for which records of infestations are less complete include:

Chinquapin burn (220 acres).—Beetle-caused losses increased 475 percent the first year after fire, decreased the second year, and increased again the third year.

Snake Lake Light Burning Experiment (200 acres).—Losses increased 1,465 percent the first year and were still 915 percent above the prefire level the second year.

Aspen Lake burn (8,000 acres).—Losses increased only slightly the first and second year after fire, probably because of salvage of fire-injured trees in the burn and direct control work in adjacent areas.

Tubbs Hill burn (30 acres).—Heavy concentration of the western pine beetle and the Oregon pine engraver was rated the first year after fire, a decline of infestations the second year, and return to normal the third year.

Further analyses of these records show that:

1. As a general rule, if a fire occurs in the late spring or early summer, some concentration of infestations within a burn develops by late fall of the same year.

2. If a fire occurs late in the summer or in the fall, beetles do not concentrate within a burn until the season following the fire.

3. During the second season after a fire, beetle-caused losses usually continue at a high level, increasing over the preceding year in some cases and decreasing in others.

4. The third season after a fire, losses usually show a reduction; by the fourth season they decline to the prefire level or below.

5. Concentrations of beetles following fires have reached spectacular proportions in some cases. On burns where accurate records have been maintained, the annual beetle-caused loss during the first and second years has ranged from 4 to 46 times the amount of annual prefire loss on the same area.

6. The intensity of beetle concentrations and the cycle they follow have varied in the different burns that have been studied. This can be accounted for by the type of burn, the timing of the fire, and the degree of crown injury in trees that survived the fire; as well

as, the weather and timber stand conditions at the time of the fire and the natural cycle of infestation in the area.

7. Where there has been prompt salvage of fire-injured trees, only slight increases of western pine beetle infestations have occurred within the burn.

In the Surrounding Areas

Where do beetles come from that are attracted to burns, and where do they go when the large concentrations begin to die down? And are beetle populations that build up in burns a threat to adjacent timber? These questions were raised during the "light burning" controversy and were among the first to be investigated in the fire-beetle relationship.

Before the Mistletoe burn, an annual inventory of the volume of loss had been made in the burn area and the adjacent pine type of the upper Rogue River Valley, and the distribution of all beetle-killed trees had been mapped. After the fire in the late fall of 1917, loss inventories were continued through 1918, 1919, and 1920. In order to determine the distances to which the influence of the fire extended, the entire area of the pine type was laid out in zones 1 mile wide extending 6 miles from the borders of the burn. The annual losses from 1917 to 1920 were computed and mapped separately in each of these zones. The results as summarized by Miller and Patterson (*99*) indicate that the effect of the burn upon the surrounding infestation could be detected for a distance of about 3 miles:

> Records thus obtained show that for the general area surrounding the burn there was slight tendency toward increase of infestation during the season of 1918 (the year following the fire), but at the same time the zones within 3 miles of the burn registered a perceptible decrease. During 1919, however, when the volume of infestation within the burn decreased 74 percent, the first zone immediately adjoining showed an increase of nearly 60 percent, while in all zones beyond this there was a very marked decrease during the season.
>
> From this evidence it would appear that the natural tendency of the infestation was to increase in 1918 and to decrease during 1919. These natural tendencies were disturbed, however, by the attractiveness to the beetles of the fire-injured trees in 1918, which caused many beetles to leave the first three surrounding zones and concentrate in the burn. In 1919, as the attraction of fire-injured trees had subsided, some of the beetle population which had concentrated in the burn attacked trees in the area immediately adjoining, causing a perceptible increase locally although all other areas registered a decrease.

The 1919 increase in the zone immediately surrounding the burn, although perceptible, did not develop into a serious epidemic. What occurred was a local interruption of the infestation cycle, and normal trends were restored within 3 years after the fire.

The Northfork burn study has supplied data to show that the influence of a burn upon the rate of loss in adjacent timber is not

always perceptible. In this study, the cycle of infestation from 1919 to 1926 within the area of the 5,400-acre fire was compared with the cycle in an adjoining check area of 1,880 acres. This comparison, shown by figure 50, is discussed by Miller (*U196*):

> The outstanding point brought out by this comparison is that the cycle, both preceding and after the fire, was essentially the same in both areas. They differ mainly in the relative quantity of the losses during the seasons of 1924, 1925, and 1926. The severe drought of 1924 resulted in a great increase of beetle losses throughout the Sierra pine belt which is reflected in the record for the Cascadel area. This increase reached its peak in 1925 and a pronounced drop occurred in 1926 in both areas. On the burn, however, the increase in 1925 was boosted far beyond what would have occurred normally as a result of the drought alone, but the decrease in 1926 was much greater in proportion than that on the Cascadel area.

Although these studies indicate that serious infestations do not normally spread out of burns into adjoining areas, data from surveys and other sources indicate that in certain cases a widened attack may occur. A report by Salman (*U258*), referring to the 1930 survey of the Coulter pine type on Palomar district, Cleveland National Forest, Calif., states:

> In 1928 a fire burned out a portion of the stand in Dyche Valley and evidently scorched some of the timber, providing material in which it was possible for the western pine beetle to breed. The beetles emerging from this material apparently spread to unscorched timber outside of the fire area and have continued their intensive attack until at the present time an area of approximately three-fourths of a section has suffered a loss of 65 percent of the stand.

A similar development in the Coulter pine type, involving an *Ips*–western pine beetle outbreak, was reported by J. M. Miller in the 1941 survey report of Cleveland National Forest:

> This infestation apparently originated around the eastern border of the 1938 burn where it was localized in the fall of 1939. In the fall of 1940 large groups were noted in the area west of Julian which had been relatively free of infestation previously. New groups were also found springing up in the Pine Hills unit to the north, which are also part of the spread from the original center around the burn.

Besides the burns in the Coulter pine type in southern California, there have been several burns in the westside pine type of the Sierra from which western pine beetle infestations were believed to have spread into adjoining timber. One of these was the 1941 Power Line burn in the southern part of Yosemite National Park. G. R. Struble reported upon the conditions around this burn in 1943:

> Groups of ponderosa pines killed by the western pine beetle were evident, particularly along the Wawona road from Chinquapin to the Valley and in the vicinity of Big Meadows. Activity is centered in the vicinity of Big Meadows burn which occurred

512690—60——16

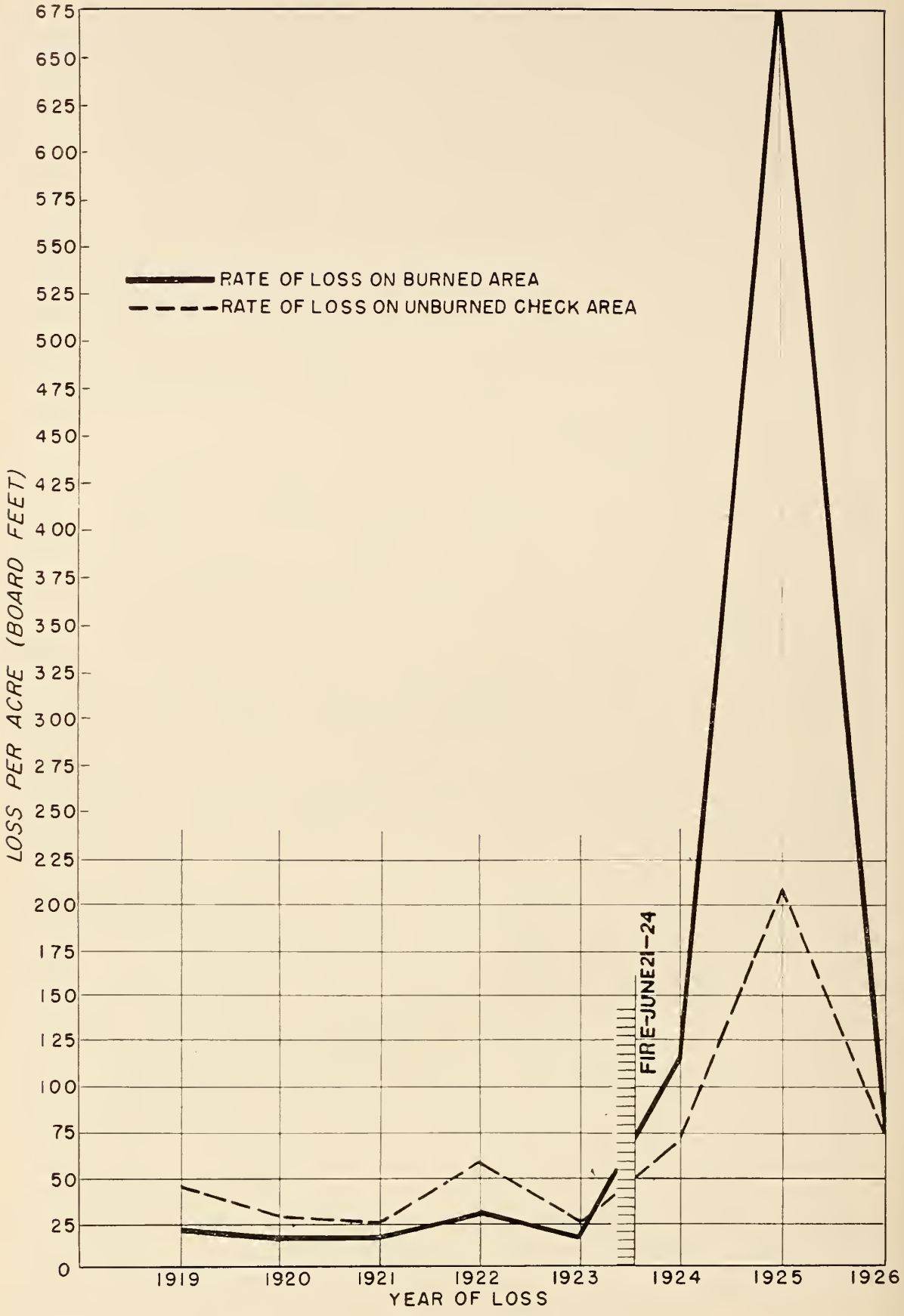


FIGURE 50.—Comparison of pine volume killed annually by bark beetles on burned area (5,460 acres) and on adjoining check area (1,880 acres). North-fork Burn, Sierra National Forest, Calif., 1919–26.

in October 1941. In the burned area and adjacent to the burn, hundreds of recently faded trees were observed.

This report indicates that the greatest spread of infestation occurred the second and third years after the fire and extended from the borders of the burn to areas 6 miles distant. Other fires for which data indicate a spread of serious infestations include the San Joaquin canyon fire on Sierra National Forest in 1939 and more recently the Black Rock fire on the same forest in 1943.

On the other hand, evidence from many other records shows that burns from which no spread of infestation could be detected represent the majority of burns that have come under observation. Timing of a fire according to season, brood success in fire-injured trees, susceptibility of trees in unburned areas, climatic conditions, and the natural trend of infestations can be suggested as possible factors influencing the potentialities of infestations becoming aggressive in surrounding timber. This phase is one that has been given little study, and much more information is needed before definite conclusions can be drawn.

Long-Term Effect of Burns

Although a fire of moderate intensity in ponderosa pine stands immediately sets up conditions favorable to western pine beetle populations, it does not hold that these conditions persist long after the fire. Changes in the ecology of pine stands may develop in the lighter types of burns which would be unfavorable to continuing infestations. This was one of the contentions of the proponents of "light burning."

Within a period of 3 to 5 years after a moderate fire, most of the susceptible fire-injured trees have been killed, the stand of larger trees has been thinned, much of the competition of the older trees with the understory of brush and reproduction has been reduced, and the surviving trees are making vigorous growth (fig. 46). All studies that have been made of the ecology of the western pine beetle indicate that such conditions reduce the hazard of bark beetle attack.

Some foresters have considered the use of controlled fires in ponderosa pine stands as a silvicultural agent for reducing both fire and beetle hazards. This theory was advocated by Weaver (*142*) in 1943. Weaver's main argument against total fire exclusion in mature pine stands was stated as follows: "It is believed that the dense stagnating stands of reproduction that have developed on vast areas have aggravated the beetle losses tremendously as a result of their competition with the larger trees for the limited soil moisture."

Since 1943, Weaver has not only argued the case for "prescribed burning" in ponderosa pine stands, but has tried it out on Colville Indian Reservation of northern Washington and on Fort Apache Indian Reservation in Arizona. The results have been generally beneficial, particularly from the standpoint of fire hazard reduction (*143*).

Forest insect survey men have made repeated observations on the relationship of competing vegetation and beetle-caused losses in

the interior type stands of ponderosa pine where soil moisture is such a critical factor. A high rate of tree mortality usually occurs in mature stands containing a dense understory of stagnated reproduction and brush. There usually is light beetle damage, however, in areas where fires of past years have removed the competing understory. These lighter losses only occur after a flareup of beetle activity in fire-weakened trees during the first 3- to 5-year period immediately following a fire.

Keen compared beetle damage on two adjacent areas of the Happy Camp district of Modoc National Forest, Calif., in 1926. One of these areas had been burned 7 years before by a fire that removed most of the understory but made no reduction in board-foot volume of the reserve stand. The other area was unburned. Pine beetle damage was extreme throughout the unburned stands, but light on the burned area. The reserve pine volumes on the two areas were essentially the same. The beetle-caused losses on the two areas were compared as follows:

	Estimated number of trees killed per section	
Unburned plots:		
Heavy understory of brush and reproduction	*1925* 200	[1] *1926* 250
Plots burned in July 1919:		
Ground with no brush or reproduction	40	20

[1] Summer.

On the South Ice Cave Fire of Deschutes National Forest, Oreg., forest officers studied the long-term effect of fire upon conditions that relate to bark beetle hazards in pine stands. These studies extended over a period of 22 years from 1915 to 1937. Keen (*U163*) summarized conclusions from a 1937 examination of the study areas:

> Analysis of stand conditions on the 1915 burn and in the surrounding areas indicated a larger number of trees per acre off the burn, but a larger volume per acre on the burn, in trees of larger diameter and volume per tree. Stand structure analysis showed a dearth of younger age classes on the burn and with a higher percentage of trees in beetle-susceptible classes than in neighboring areas.
>
> From a snag count and check of current 1937 pine beetle damage, a somewhat heavier loss of timber was noted outside the burn than inside, but the variability between plots was too large to permit conclusive data on this point.

Thus in general, the long-term effect of fire is to lessen western pine beetle damage rather than increase it.

SECTION IV. WESTERN PINE BEETLE SURVEYS

HISTORICAL

Pine beetle surveys are for the purpose of finding what species of bark beetles are causing timber losses, where infestations are located, and how much timber is being destroyed. Research and control work are both guided by this basic information.

Hopkins' (*42*) western trip in 1899 appears to be the first undertaking that can be classed as a survey to determine the existence and importance of the western pine beetle. This was followed by Webb's (*144*) work in Idaho in 1904–05. These preliminary surveys did not attempt a measurement of losses or delineation of areas infested, but they did establish the importance of the beetle as an actual and potential threat to pine resources.

Some years later (about 1910), private timber owners and public land-managing agencies began to recognize the importance of the problem. In order to know just how much timber they were losing and what could be done to reduce the loss, owners and agencies started the first quantitative surveys. At about the same time, the Bureau of Entomology began the measurement of beetle-caused losses on selected areas to serve both its research and control activities. Gradually these surveys were expanded into an annual program that now covers with varying degrees of intensity most of the western pine region (*38*).

The methods used in conducting pine beetle surveys have varied widely. The most elementary method, used by Hopkins and other pioneer investigators, was merely to view an area from a vantage point or by reconnaissance to gain an impression of the extent and character of losses. From this elementary approach, modern methods have developed using timber estimation techniques adapted to beetle-killed timber.

Klamath River Survey, 1911

The first intensive survey to measure the amount of beetle-killed timber was the "Little Humbug Creek" survey on Klamath National Forest just west of Yreka, Calif. Because of the apparent depletion of ponderosa pine stands in the Klamath River watershed, Forest Assistant A. H. Hodgson (*U100*) made a survey of five sections to "gather accurate data regarding the topography, condition of timber, general history of the area, and an estimate of green and dead timber on representative sections where yellow pine, sugar pine, and Douglas-fir are infested and being damaged by insects."

Pioneering a new technique, Hodgson (*U100*) ran a 10-percent strip through each 40-acre subdivision of the area:

> The crew consisted of three men, a compassman who ran the line, sketched topography, and made an ocular estimate of the timber; and two tally men. The dead timber was classified as

white tops, *red tops*, *black tops*, *standing snags*, and *down snags*. The compassman also located for each entire section the white tops or trees freshly attacked by the western pine beetle.

Two tally men found or "spotted" infested trees while a compassman located them on a map. Thus Hodgson was probably the first to prepare a "spotter's" map by fixing the location of each infested tree with a "spot" or tiny circle on a survey map.

The total depletion of pine measured on these sections in 1911 ran into formidable figures, averaging from 40 to 50 percent of the stand on some of the area (*89*) and from 10 to 20 percent on the less heavily infested sections. Miller (*U176*) estimated that "the total loss figures for dead yellow pine represented the accumulated loss of about 30 years."

The Klamath-Lake Counties Surveys, 1911–20

Private timber owners of Klamath Falls, Oreg., were among the first to become interested in bark beetle control. About 1910 Jackson F. Kimball of the Klamath-Lake Counties Forest Protective Association began to inquire into the problem, and in 1911 he started preliminary bark beetle surveys in some of these areas. The Bureau of Entomology established a field station at Klamath Falls in 1912 and furnished technical assistance to the Protective Association in locating infested trees for the first control project located in the Parker's station tract. For some years, the Association maintained an annual surveillance of its holdings to locate areas where bark beetles were active, assisted in this work from 1914 to 1919 by W. E. Glendenning, Agent for the Bureau.

Control Surveys by the U.S. Forest Service, 1912

The first control projects undertaken by the Forest Service in California were started on Klamath, Sierra, and Trinity National Forests in 1912. A number of reconnaissance surveys were made to determine the need for further control and to spot for actual control operations. The more important of these surveys were made by Forest Examiner Ralph Hopping.

In 1913 the regional forester established the requirement for an annual report concerning current insect conditions for each national forest. Still required from each district ranger, these reports were then based upon general observations or upon factual surveys where necessary. This information was supplemented, however, by a considerable amount of more intensive survey work by personnel at the forest insect field laboratories.

Rogue River Surveys, 1915–24

Beginning in 1915, the Ashland station of the Bureau of Entomology conducted a series of quantitative surveys to serve as a basis for studies of the biology and epidemiology of the western pine beetle, and also to test the accuracy of survey methods. (See de-

scription in Section II, p. 130.) The more pertinent survey reports are by Miller (*U178*, *U181*) and Patterson (*U221*). The method of survey was to view units of the area topographically, then count and map the insect-killed trees. Certain parts of each watershed were also cruised intensively, and all infested trees were examined and marked. Then an estimate was made for each area based upon results of the extensive viewing and adjusted by the results obtained on sections that were intensively cruised. The project area was concentrated in units of the Rogue River watershed near Ashland where loss records were maintained for the entire period of the study. Surveys from 1916 to 1918, including parts of the Applegate and Klamath River watersheds, covered a total area of 350,000 acres.

The California Survey, 1917

Before 1917 most bark beetle surveys were made in areas where unexpected or spectacular infestations had aroused concern of the timber owners. These surveys were usually made as the first step in the initiation of control. The first overall appraisal and analysis of conditions within a general subregion was the cooperative "California Survey of 1917," undertaken as the result of agitation among a group of lumber companies that were disturbed over damage caused by bark beetles. Some advanced the idea that infestations were increasing because of total fire suppression, a policy then becoming established on Federal and private timberlands. In January 1917, three of the larger lumber companies and the California Forest Protective Association petitioned the Secretary of Agriculture to "make an immediate investigation of the extent and seriousness of the loss caused by bark beetles."

This 1917 survey was organized under the direction of the Bureau of Entomology, with the Forest Service contributing the time of three of its technical men and the Bureau detailing four men to the work. Private owners, the Forest Service, and the National Park Service financed examinations on the land each managed. The area covered included the western slope of the Sierra Nevada from Rubicon River to the South Fork of Tule River. The project was completed in the summer of 1917, and the accomplishments and recommendations of the survey were presented in a series of reports by Miller, Hopping, and Jaenicke (*U202*).

According to preliminary report, the methods used "consisted of extensive cruising, supplemented by sample plots from time to time which furnished the necessary data for the proper interpretation and significance of the counts obtained in the extensive cruises." Usually the Forest Service and Bureau men worked in field parties of two men each, or singly with the assistance of local representatives of the cooperating agencies.

The summarized results of the 1917 survey included the following:

Period of survey	June-October 1917.
Total acreage of pine type examined	1,682,000.
Stand of pine timber represented (ponderosa, Jeffrey, and sugar pine).	19½ billion board feet.
Total pine loss estimated	25,570,000 board feet.
Cost of fieldwork, salaries and expenses	$3,200.

Southern Oregon-Northern California Project Surveys, 1921–24

Concern over rapidly increasing infestations in the Klamath Basin reached a climax in 1920 and brought about the start of a large cooperative control project in 1921. The project eventually encompassed 1¼ million acres of pine timberland protected by the Klamath Forest Protective Association, the Indian Service, and the Forest Service. As a basis for control plans, it was necessary to assemble all available information on losses and stand conditions. The three agencies furnished their file information on stand conditions, and A. J. Jaenicke carried on only enough reconnaissance work to interpret this information (*U102*).

In the fall of 1921, a detailed loss survey was made, and the project area was divided into control units. In the next 2 years, the project was organized into a series of reporting units and areas on which records were maintained through the 1932 season. The survey program for the project originally included 34 check sections, a total of about 21,000 acres, supplemented by roadstrips and topographic estimates. Besides obtaining an overall appraisal of infestation conditions for the entire area, this continuing annual survey aimed to determine results of the control work and the need for further work, and to provide a basis for planning action programs. The first summaries of these surveys were prepared by Keen (*U139*).

The main cooperative phases of the project were terminated in 1924. However, loss surveys were continued annually by the Bureau of Entomology as a basis for research projects and for control recommendations. Keen (*U149*) prepared a long series of annual survey reports on this project.

Regional Forest Insect Surveys

The Forest Service early recognized that protection of national forests from insect depredations was one of the responsibilities of a forest ranger. Efforts were made to get the rangers to report unusual insect activity to the forest supervisor, who in turn would report conditions to the division of timber management of the regional forester's office. Hopping's (*49*) manual of 1914 called for such reports on cutover lands. Later report forms, developed by the regional foresters with the help and advice of the Bureau of Entomology, were intended to be submitted by the rangers on an annual basis. Some of these reports were of value in calling attention to insect outbreak conditions; others were too perfunctory to have much value. Though not entirely successful, such reporting has been continued in one form or another with the hope of encouraging rangers to learn more about insect problems and forest protection responsibilities.

Starting about 1930, the Bureau of Entomology in cooperation with the Forest Service, the Park Service, the Office of Indian Affairs, and other land-managing agencies endeavored to expand annual forest insect surveys on a regionwide basis (*110*). The plan envisioned coverage of all the more important forest insect infesta-

tions in five Western States: California, Oregon, Washington, Idaho, and Montana. The object was to obtain information annually concerning the intensity and trends of forest insect infestations (particularly bark beetles) in these States, both for study purposes and as a guide to the need for control work. The survey planned two phases: (1) preliminary scouting and detection reports by fieldmen and forest officers of the different land-managing agencies; (2) quantitative appraisal surveys of the Bureau of Entomology alone or in cooperation with these agencies or private timber owners.

For many years the regional survey program was largely confined to the interior ponderosa pine type where western pine beetle outbreaks were progressing. Funds and personnel were not available for the Bureau to conduct complete regional coverage. Consequently the annual appraisal survey was concentrated where the beetle problem was of most significance, including commercial pine stands that were being depleted and recreational tracts where the maintenance of tree cover was considered to be important. Other forest insect outbreaks were noted whenever observed, and some were covered with intensive appraisal surveys if they appeared to be serious and control action was contemplated.

Since the passage of the Forest Pest Control Act in 1947, the forest insect survey program has been enlarged to cover all forest areas and all species of destructive forest insects. Detection of outbreaks has been strengthened by enlisting all forest personnel into an expanded team to detect and report unusual insect activity. In addition nearly all forest areas are covered annually by aerial reconnaissance to supplement ground observations. An increased amount of general information is now being obtained on more locations so that nearly all forest areas are given some degree of insect protection. This expansion in coverage, however, has reduced intensive sampling for some insects. such as the western pine beetle. Yearly records of western pine beetle infestation trends came to and end in California in 1948 at a time when surveys for other forest insects were expanding.

In recent years fieldmen of all Federal, State, and private forestry organizations have been enlisted in this regionwide forest insect detection survey effort. Their reports of forest insect outbreaks and recommendations for control are transmitted through their administrative organizations to the Division of Forest Insect Research of the Forest Service, where the information is assembled and summarized. Final recommendations for control action are usually passed upon by local pest-control action groups if the proposed control work involves forest land under more than one administrative jurisdiction. Control work is usually carried out by a land-managing agency under technical guidance of forest entomologists.

Research Objectives of the Regional Surveys

In addition to providing an annual record of the intensity and trends of bark beetle damage for possible use in control programs, regional surveys have often included research objectives. In many, research information of outstanding value has been obtained as a

byproduct of the survey program. Salman (*259*) defined two research objectives of the California regional survey:

1. To attempt to correlate intensity and trends of forest insect infestations with physical factors of climate, soil, altitude, topography, the biotic factors, etc.
2. To obtain information concerning effects on a stand of heavy infestations, particularly as regards changes in the susceptibility of the stand.

The study of tree susceptibility (*68*, *71*), climatic cycles as indicated by tree rings (*69*), and the rate of falling of ponderosa pine snags (*65*, *78*) are examples of research findings made possible by the regional survey program.

Regional Reports

As data have accumulated from regional surveys, occasional summaries have been issued for each region to show the overall picture of forest insect infestations and interpret the conditions. Reports covering annual status of western pine beetle infestations in the western regions are available in the files of the Division of Forest Insect Research of the U. S. Forest Service experiment stations at Berkeley, Calif.; Portland, Oreg.; and Missoula, Mont.; or in the central office in Washington, D. C.

Forest insect condition reports for the California region have been issued for 1931, 1931–36, 1937, 1949, 1950, 1951, and subsequent years. Reports covering Oregon and Washington have been issued for 1933, 1933–38, 1938–42, 1950, 1951 and yearly since then. Yearly reports for Idaho and Montana are available for the period 1927 through 1951, and for 1955. A national summary of the more important forest insect infestations, including the western pine beetle, has been issued annually since 1950 by the Washington office of Forest Insect Research, U. S. Forest Service.

Hazard Zonation

Studies carried on in conjunction with bark beetle surveys in the eastside pine type from 1931 to 1935 began to point the way toward the recognition of susceptibility to bark beetle infestations in certain areas and timber types. Therefore still another type of survey was developed to appraise and zone timber stands according to potential losses (see Section III, p. 206). Such surveys have immediate practical value for land managers because they point out areas where much of the potential loss can be avoided by prompt sanitation-salvage logging.

The first survey of this character, undertaken on Lassen National Forest of California in 1936, was mainly a tryout of methods and ideas that had been developed up to that time. In this survey, the Eagle Lake tract of some 23,000 acres was zoned according to five degrees of hazard. The report prepared by Salman and Johnson (*U287*) included recommendations for treatment of the area.

This preliminary work on hazard rating met with the interest and support of the pine operators, and in the fall of 1937 the same type

of survey was organized to include the entire eastside type of northeastern California. The purposes and methods of this survey were described by Johnson (*U125*) (*56*). Progress reports on the results of the hazard-zonation program were issued to cooperators each season as units of the area were completed. The program was finished in 1940 after four seasons of fieldwork and eventual coverage of 2¼ million acres. The final summary was prepared by Miller, Salman, and Johnson (*100*).

Lacking funds to conduct similar field surveys of hazard in eastern Oregon, Keen analyzed existing office data from timber surveys and annual insect loss surveys. On the basis of this analysis he prepared preliminary hazard appraisals in 1939 for the Klamath subregion of 2,580,000 acres (*U154*), and in 1941 for the Deschutes subregion of 1,725,000 acres (*U161*).

In the period 1945–48, several hazard-zonation surveys were made of ponderosa pine stands in eastern Oregon by J. M. Whiteside of the Portland Forest Insect Laboratory. These included the Sisters area of Deschutes National Forest (*U334*), the Snow Mountain area of Ochoco and Malheur National Forests (*U337*) and Warm Springs Indian Reservation (*U336*). On the Sisters area, quarter-acre circular plots spaced at 330 feet along section lines were used to sample stand hazard conditions. On the Snow Mountain and Warm Springs areas, 1-chain-wide strips were cruised from the fender of a car.

Using a frame in which three tally registers were mounted, the surveyors made counts of (1) all green trees (except Keen's age class 1) further segregated into (a) low-risk trees with a penalty score of four or less (table 6, p. 189) and (b) high-risk trees with a penalty score of five or more; and (2) all snags of merchantable size. By this method, from 0.5 to 0.75 percent of the areas was sampled. At the same time, a visual appraisal of site and stand conditions was made. The areas were then mapped in the field by five hazard zones largely on the assumption that the percentage of risk trees in the stands offered the best measure of hazard.

In 1951 Furniss (*U61*) led a hazard survey of 95,000 acres of old-growth ponderosa pine in the eastern part of Lassen National Forest of California, using the hazard regression formula developed by Keen and Merriam (*U172*). Cruise lines were located 40 chains apart, and one-half acre circular plots were located at uniform 10-chain intervals along a compass line. Plot data included volume of pine per acre, number of Risk 3 and 4 trees, past loss, and degree of competition from pole stands and brush. Degree of hazard was then computed by formula for each plot, and the relative hazards of each unit of the area were determined. Because of extensive cutting in the eastside ponderosa pine type, this was one of the few remaining areas of virgin pine in northeastern California where hazard surveys would yield information of value in deciding order of cutting.

Bark Beetle Survey Manuals

The need for a bark beetle survey handbook was recognized soon after control work started. The first instructions on survey methods appeared in a manual by Ralph Hopping (*49*) issued by the Forest

Service of District 5. This manual was fairly specific and detailed in its instructions for conducting control work, but survey methods were treated only under "spotting," that is marking the infested trees to be treated on control projects. In the appendix, Hopping listed points that should be taken into account and reported upon in "forest insect reconnaissance," a term used for precontrol surveys. The greater part of the manual was taken up with information on the more important tree-killing insects, causes of infestation, and special instructions and reporting forms used in control work.

A short article by Miller (*91*) in June 1925 discussed the purposes of forest insect surveys and the methods used up to that date.

Two manuals by Keen (*59*, *61*), prepared in 1926 and 1927, included detailed instructions on the organization and methods of making bark beetle surveys, as well as on organizing and carrying out control projects. The second edition, included a complete discussion of the problem of obtaining adequate information on current infestations and estimates of loss, and provided detailed instructions for sample plot work. The costs of survey and the accuracy to be expected were presented in tabular form. This manual included several useful charts and reference tables, such as (1) number of trees and acres ordinarily spotted per day by a three-man spotting crew, (2) chart of open seasons for bark beetle control by species and regions, (3) measurements for construction of a Biltmore scale, (4) total bark surface for each diameter and height of tree, (5) comparative accuracy and costs of different types of surveys, (6) sample forms used in mapping, marking, and tabulating infested trees, and (7) the reporting forms used in different types of surveys.

In 1933 Keen and Jaenicke (*134*) prepared a forest insect handbook for use in the North Pacific Region. This handbook, designed to apply to all of the more important forest insects of the area, discussed surveys for research purposes and for control. Detailed instructions were given for the operation of a three-man survey crew in spotting, mapping, marking, and recording infested trees; for the preparation of annual reports required of forest officers; and for the selection, setting up, and measurement of losses on sample plots. Tables were included for determining the period of attack of infested and recently abandoned trees.

Johnson (*54*) prepared a field manual of bark beetle survey methods in 1935 for use primarily in the development of the California survey program. This manual contained instructions for intensive and extensive types of surveys, and it outlined the organization, procedures, and equipment used in establishing and measuring losses on permanent sample plots. The methods of marking plot boundaries and strip cruise lines on regional survey plots were described in detail. This manual is the only one that provides for the setting up of plots on cutover lands; it is also the only one giving instructions for analysis of infestations by bark-surface measurements, otherwise known as "stem analyses."

The appendix contains (1) tables for correcting compass alinement, (2) symbols to use in designating forest type, (3) definitions

of site index, (4) definitions and illustrations of the Dunning and Keen tree classes, and (5) descriptions of infestation types. The correction factors for estimating the total seasonal loss inventoried at any date are shown by curves for Modoc and Lassen National Forests and for the westside Sierra pine region. Sample forms for records and reports and instructions for their use are included.

Buckhorn (*13*) prepared a handbook of instruction in 1944 for the establishment and annual checking of 320-acre plots in mature virgin pine stands of Oregon and Washington. Chief purpose of this handbook was "to facilitate the training of personnel and improve the quality of the work" in the use of standardized methods of plot surveying. The organization of a three-man crew and duties of its members were treated in detail.

The manual contains keys for the identification of beetle-killed trees according to the year in which they were attacked; instructions for the use of the compass, Biltmore stick, and other survey equipment; and the sample forms for recording and reporting of data. It also includes a set of original volume tables for both green and insect-killed ponderosa pine on different sites as developed from height curves from sample-plot measurements in eastern Oregon.

Buckhorn (*13*) describes the method of risk-rating trees by the use of "penalty scores" for individual tree health characters, the method Keen developed as a supplement to his bark beetle susceptibility classification. This manual also describes the Keen tree classification slide rule (*73*) and its use in checking the classification of borderline trees.

Other references to forest insect survey methods are contained in the textbook "Forest Insects" (*30*) and in "Insect Enemies of Western Forests" (*75*). In the latter, forest insect surveys are grouped according to their intensity and purpose and are classed as (1) "detection of bark beetle outbreaks" by the field officers of land-owning agencies, and (2) "extensive bark beetle surveys" to determine the intensity, size, and character of the infestation and whether control operations are justified. Under (2), both topographic and sample-strip methods are described.

SURVEY METHODS

Most bark beetle survey methods evolved out of practical experience with forest mensuration techniques as applied to beetle-killed timber, with such modifications as were needed to provide for the collection of entomological data. In practice, methods are modified to fit forest types, infestation characteristics, seasonal conditions, and the particular purposes for which the information is to be used. Survey methods have been studied critically at times by forest entomologists to evaluate their efficiency, relative costs, and the possibilities for improvement. The phases considered include (1) the units by which the quantity of infestation is measured, (2) the methods of area coverage, and (3) the correction factors used in formulating estimates.

The Units of Loss Measurements

The entomological purposes of bark beetle surveys usually require that the amount of the infestation be expressed in some quantitative way. This can be done by using units of measurements to express either (1) the number of trees or volume of timber killed, or (2) the quantity of beetle population occurring on an area at any one period.

The Number of Infested Trees

The simplest way to express the amount of infestation within an area is by a count of the number of infested and recently killed trees. The advantage of a simple tree count is the ease with which it can be used in visual surveys. If all of the trees were of uniform size within an area, this unit would serve as a satisfactory basis for computing loss volume and the amount of infested bark surface representing beetle population. However, infested trees vary greatly in size within the same area and between areas. Consequently, the number of infested trees does not usually give a true quantitative picture of western pine beetle infestations unless tree size and volume are known and totaled.

Regardless of quantitative accuracy, the number of trees killed annually per section is a unit commonly used on all reconnaissance surveys. An experienced estimator often can arrive at a useful estimate of the number and average size of beetle-killed trees within an area and thus translate his visual counts into estimates of timber volume lost.

The individual infested tree, regardless of size, must be regarded as a biological unit, because it is the center of attraction for a large number of attacking beetles and the localized breeding place for a seasonal generation. In control work, each tree must be located, felled, burned, or otherwise disposed of. Consequently, it is important to know the actual number of infested trees within an area as well as their total volume, and these items always are important elements in survey data.

Board-Foot Volume

The need for board-foot volume data in the expression of beetle-caused losses has led to the almost universal practice of measuring the diameter and height of each infested tree in bark beetle surveys. This may be done for all trees within the area (as on a control project) or on selected sample plots only.

Loss in Relation to Acreage

"Board feet per acre" is a derived unit which has often been used as an expression of intensity of loss. It is a measure commonly used by foresters and easily visualized by them. It is also easily computed once the number of trees killed, their volume, and their acreage are known. It can be accepted as a fairly good comparison of the intensity of loss between areas where stand conditions are comparable. The disadvantage of this unit is that it does not give a true comparison of infestation intensity when the stands are not equal, i.e., where type or volumes differ or where large areas of nontimbered or non-

pine type forest land are involved. For instance, the loss of 100 board feet per acre in a stand of 5,000 board feet of pine per acre is of much higher intensity than the same loss in a stand of 25,000 board feet per acre. In the first case, such an infestation would be considered epidemic: in the heavy stand it would be rated only endemic.

Loss in Relation to Stand Volume

For comparative purposes the percentage of stand volume killed—the volume of loss divided by the stand volume—gives the best index to the intensity of losses. Percent of stand killed gives a ready comparison with growth percent and also indicates the degree to which stands are being depleted. Although this unit is probably the most useful in showing the seriousness and progress of bark beetle infestations, its use is limited by the lack of available or reliable stand volume data in many areas. Another disadvantage is that where heavy losses or cuttings are depleting the stand, the base on which the percentage is computed is changing and has to be revised from year to year. This change also prevents the addition of yearly percentages in order to arrive at the total percent of stand killed over a period of time.

Infested Bark Surface and Unit Trees

Forest entomologists have also devoted some effort to finding a unit that would serve as a more accurate measure of the quantity of beetle population. On the average, the infested bark surface of a given tree has a direct relation to the number of beetles that attack and emerge; thus it can serve as a beetle population indicator. If a unit tree represents a constant area of bark surface, it can be used as a fairly reliable measure of beetle population provided we assume that on the average a square foot of bark has about the same population from year to year. Since we know that population density per square foot varies from tree to tree and from one generation to the next, unit trees cannot be converted to beetle populations without a great deal of sampling.

In 1915 Keen (*U133*) carried out a series of surveys near Ashland, Oreg., in which he used infested bark surface and a hypothetical "unit tree," based upon a constant area of infested bark, as a unit representing beetle population. In order to facilitate the computation of bark surface area from survey records, he prepared a table giving the total bark surface for each tree of a given diameter and height. Where more than one species of beetle occurred in the same tree, the amount of bark surface occupied by each was apportioned by measurements or estimates of infested lengths. Noninfested bark areas also were computed. These bark areas were then totaled by species and the totals divided into unit trees composed of a fixed number of square feet of bark surface.

The idea of using a standard unit tree was first proposed in the supplement to a survey report on the Applegate watershed in 1916 (*U173*). Specifications suggested in this report were for a unit tree 24 inches d.b.h., 80 feet high, and covered by 50,000 square inches (347.2 sq. ft.) of infested bark. In the final summary of quantitative studies on the Lamb's Mine area (*U133*), a somewhat smaller unit

tree was used with the following specifications: 80 feet high, 200 square feet of infested bark surface. The 1915 overwintering infestation on the Lamb's Mine area was totaled by this method and expressed as follows:

	Item
Number of infested trees	217
Area of infested bark surface, square feet	45, 514
Number of unit trees (200 square feet each)	227. 57
Infestation by species:	*Unit trees*
Western pine beetle	188. 60
Other bark beetles	8. 90
Unknown	30. 07
Total unit trees	227. 57

The purpose of a standard unit tree in bark beetle surveys was to provide a unit of measurement that would compensate for the great variation in the size of infested trees and lack of uniformity in the infestation occupying the infested bark surface. Although the idea of the "unit tree" is basically sound, it has never come into general use because of the labor of obtaining measurements of infested bark surface and of converting these basic data into an arbitrary standard. Such a standard would be intelligible to only a few people outside of this special field.

Methods of Area Coverage

As the first step in making a bark beetle survey, a method must be selected for area coverage so that all or a part of the infested trees can be seen, examined, or measured. The methods of coverage used to date have been designated as (1) topographic surveys—also called topographic reconnaissance, (2) sample plot surveys, (3) road strip surveys, and (4) aerial surveys.

Topographic Surveys

Keen (*61*) gives the following description of this method:

> The estimator, equipped with binoculars and a topographic map of the area, 'gridirons' the country by traveling along the ridges or open valleys or wherever an unobstructed view may be had of most of the timbered area. At selected points along the route, the opposite slopes or areas visible and not more than 2 miles away are viewed either with the naked eye or with the binoculars, and the red, sorrel, or faded trees counted. These are then spotted on the map within the area which has been viewed, either by dots or numbers, to indicate the number of trees that have been counted. All the country that can be viewed is covered in this manner.
>
> To determine what percentage of the trees have probably thus been counted, a check plot which has previously been viewed should be intensively cruised and the ratio between actually infested trees and the number viewed on this area determined. Experience has shown that in general through the western yellow pine type, the number of discolored trees counted by the viewing method on slopes not more than 2 miles away will have to be multiplied by two to arrive at the approximate number of infested, dying, or dead trees on the ground.

Topographic surveys as bases for quantitative estimates were first described by Keen and Patterson (*U173*) in a survey report of the Applegate area, Oreg. Later Keen (*U129*) defined the factors used in correcting estimates for topographic surveys and clarified procedure in their use:

Use of the factors.

1. Count *total* fading, sorrel, and red standing trees without regard to year of their death.
2. Multiply (trees counted) by factor for type of country seen, light, and proximity of area.

The factors:

When every tree can be seen	1.0
All of country seen, near view, good light	1.5
Broken country nearby, or moderately broken rolling country at distance; good light	2.0
Broken country, deep canyons at a considerable distance, poor light	2.5
Broken country, deep canyons at a considerable distance, dark days	3.0
Very rough country, large areas hidden from view	3.5

3. Multiply by personal factor (must be determined for the individual):

Overestimate factors	.75 to 1.00
Consistent factors	1.00
Underestimate factors	1.00 to 1.50

4. Then multiply by ratio of old and new loss as determined by actual cruise of infested standing trees on a section or several sections of timber.

In 1933 DeLeon (*U52*) used topographic methods for a permanent system of surveys on Sequoia National Park in California. He refined the method to improve the accuracy of the data and to make it possible to follow the trend of losses in the same areas year after year. Permanent observation points were established from which counts were to be repeated each season, panchromatic photographs were taken which brought out the faded and red trees, and a plane table and alidade were used in mapping the position of each killed tree. These innovations are quite adaptable to the steep topography of the southern Sierra where there are good lookout points from which to view the pine type. Unfortunately, because of personnel changes, this system was dropped after the second year and was never given an adequate test.

In general practice, where timber stands cannot be seen to advantage, as in flat or rolling terrain, general viewing of the timber is combined with or replaced by the counting of beetle-killed trees along roads, trails, selected traverse lines, or on check plots. This amounts to a sampling of the area; when enough trees are examined and measured, a reliable basis is obtained for survey estimates.

Check Plots

In the early surveys, topographic estimates were supplemented by intensive cruising of a few "check plots" on each area. On these plots all beetle-killed trees were located, examined, measured, marked, and mapped. In addition, data were collected on the insect species responsible for the death of the trees, the stage of brood development, and conditions of the broods. While such plots were originally referred to as "sample plots," they were not samples in a statistical sense, and more properly were check plots.

The tendency was to locate check plots not where average conditions prevailed, but rather where the heaviest loss occurred. Once the total loss and trends of infestation were known on one or more

check plots, even though they represented maximum loss conditions, the estimator could visually compare infestation conditions on these plots with other parts of the area and judge whether losses were heavier or lighter than the ones measured. Thus, check plots served not as samples, but as yardsticks for estimating the whole.

Keen (*61*) says that a check plot "may be anywhere from 1 to 640 acres or more in size, but usually either a half or a full section is . . . large enough to give a fair sample of conditions in the vicinity." The first extensive use of check plots was in connection with the southern Oregon-northern California pine beetle control project on which a series of 60 or more 640-acre plots were used to check on control results and the need for further work. Large plots were also used extensively by the Indian Service in bark beetle surveys on Klamath Indian Reservation until 1937.

After 1931, annual cruises were made on a large series of half-section 320-acre check plots, 40 chains wide by 20 chains long, in northeastern California, eastern Oregon, and Washington. These studies served as a basis for determining infestation trends, and also helped in making general area or regional loss estimates. The plots were large enough to include most of the variable conditions found in a sample of the pine type, and hence proved good indicators of the general rise and fall of infestations in the vicinity. They also were representative of fairly large areas of forest land on which changing forest conditions could be followed over a period of time.

Another reason for adopting the half-section plot as a convenient working unit was that under ordinary conditions it was possible for a three-man crew to cruise such a plot and carry out all details of measuring the annual loss in one day. Thus the time schedule of surveys could be planned on the basis of one day for each plot. These check plots were recognized as being too limited in number to serve as a reliable sample of total loss in the pine type, but they did provide the maximum information that could be obtained with the time and manpower available.

Sample Plots

With the advance in statistical method came a desire to put pine beetle surveys on a sound sampling basis and eliminate estimates of loss based on check plots and the judgment of individual estimators. A sample plot should represent a small part of the entire infestation area, and sufficient samples should be taken so that the average conditions can be determined with a measurable degree of accuracy.

In 1938 a field study of sampling procedure was started by R. C. Hall (*U84*) in the Burney area of Shasta National Forest, Calif. The objectives of this study were to determine the number, size and shape of plots needed to give an adequate sample of an area of about 250,000 acres. Loss records and maps of the half-section regional survey plots in northeastern California made it possible to analyze probable results by breaking these down into smaller units of varying shapes and sizes. These plots were divided into smaller units of 5, 10, 20, 40, 80, and 160 acres, and the average annual board-foot loss per acre was computed for each plot for each year over a 6-year period. Some of the results were reported as follows:

The range in loss on the smaller plots is relatively much greater for a single year than it is for the average of 6 years. (Some 20-acre plots showed no loss at all on certain years.)

Theoretically the most efficient plot size of those tested proved to be the 5-acre unit. However, the gains in efficiency of the fives over the tens and the tens over the twenties were so slight that they can hardly be considered practical.

Although there is considerable variation in the 20-acre plots, the combining of these smaller plots into large units even up to 160 acres has not materially reduced the variation and it has been found that there would still be considerable variation in 320-acre plots which are side by side.

The shape of a plot appears to have some effect on its efficiency, although only slightly so. It was found that the long, narrow plot was generally more efficient than a square one.

In 1939 a series of forty 20-acre plots was established in the Burney area, and for several years losses were measured annually. Hall (*U84*) computed the sampling error for 37 of these plots for the 4-year period 1938–41 and found it varied from 35 to 48 percent. He states: "A sampling error of about 40 percent for the whole unit of about 250,000 acres seems very high and may not be much better than a guess on the part of an experienced observer." Thus unless the coverage with small plots is more intensive than the 0.3 percent used on this area, small plots do not offer any real advantage in improving the accuracy of estimates over half-section plots for survey purposes. In both cases the plot data need to be supplemented by general observations.

It is also evident that when a series of well-distributed small plots is used, the amount of travel time between plots makes their coverage more costly than a cruise of the same amount of acreage in one or two large plots. Another disadvantage of the small plot is the greater possibility of error in deciding whether trees along the boundaries are in or out of the plot; total perimeter is much greater than that for the same amount of acreage enclosed in one large plot.

In 1951 a conference on survey methods was held at Fort Collins, Colo., by forest entomologists and others engaged in surveys (*U91*). They agreed that all intensive surveys should be so designed that a valid estimate of sampling error would be possible. It was also agreed that completely random sampling, while theoretically desirable, was not practical for most western surveys. The maximum acceptable error to be tolerated for small units was set at 25 percent at the 68-percent level. This would require a different amount of plot sampling, depending upon the size of unit sampled in western pine beetle surveys:

	Sample needed with—		*Plots needed*	
Size of unit to be sampled (acres):	*10-acre plots (percent)*	*320-acre plots (percent)*	*10-acre (number)*	*320-acre (number)*
1,000	28. 0	50. 1	28	1. 5
2,000	16. 3	33. 6	32	2. 1
5,000	7. 2	16. 7	36	2. 6
10,000	3. 7	9. 3	37	2. 9
15,000	2. 5	6. 4	37. 5	3. 0
20,000	1. 9	4. 9	38	3. 0

R. C. Hall, assisted by J. W. Bongberg and M. M. Furniss of the Berkeley Forest Insect Laboratory, and Dale C. Prentice of the Western Pine Association, carried out a field study in the spring of 1951 at Blacks Mountain Experimental Forest to test the effect of size and shape of plots on the efficiency of an appraisal of infestation of 10,000 acres of virgin eastside pine. Hall (*U90*) found that the most efficient of all methods tested was a 2½ percent sampling using half-acre circular plots established at 5-chain intervals along a compass line. A survey of this type using systematic sampling techniques is most appropriate for appraisals of limited areas where estimates are needed for control. Such intensity of coverage is not feasible for annual loss surveys on a statewide or regional basis.

Road Strips

The development of road systems throughout most commercially valuable ponderosa pine stands opened up possibilities for using road strips in bark beetle loss surveys. The almost universal use of auto transportation in forest work and the ease with which motor vehicle speedometers can be used to measure distances gives a special appeal to the use of the road-strip method over the slow, tedious pacing of section lines on foot.

In many of the early surveys, trails, wagon roads, or highways that passed through the timber type were used as lines along which the infested trees could be counted as a basis for loss estimates. In some surveys the trees along these road strips were examined and measured for a fixed distance of several chains on either side. When such a survey is run for a measured distance, the road strip becomes in effect an elongated plot. Considerable study has been given to improving the accuracy of this method, with the expectation that road-strip sample plots would replace half-section plots abandoned as they were cut over in logging operations.

Hall (*U84*) adopted the road-strip method for the Hat Creek sampling study as a check against the results obtained by the sample-plot method. On a strip 10 chains wide (5 chains on each side of the right-of-way), the beetle-killed trees were examined, marked, and mapped just as they were on sample plots. Hall also tested the road-strip method on Blacks Mountain Experimental Forest (10,000 acres) which had been previously covered by a 100-percent loss inventory. The results of this road-strip survey gave an estimate of 112 board-feet loss per acre compared with an actual loss of 102 board feet obtained by the 100-percent cruise. The road-strip survey, aided by a comprehensive network of service roads, was made in 3 man-days as against 75 man-days required to make the 100-percent loss survey on foot.

In 1941 Johnson (*U124*) established road strips to replace the rapidly diminishing number of permanent check plots in northeastern California. So that data from the strips would be comparable in accuracy to data obtained from the check plots, Johnson outlined the considerations for the selection of strips and standardized the instructions for measuring and recording data. These instructions were designed for the establishment of road strips that could be surveyed year after year for a continuing loss record:

To eliminate non-timbered and overlapping areas along roadside sample strips, 'net length' is defined as 'the timber length of that portion of the strip actually cruised,' while 'gross length' includes net length plus any non-timbered or atypical stand . . . Each strip should be sub-divided and cruised in units of one mile . . . If strips are to be permanently marked, one must at least begin the strips at known landmarks or from permanent markers along the road.

The *width of strip* is usually governed by the density of the stand and ground cover and by the topography of its cross-section. In the level, comparatively light stands of the eastside region, a strip 10 chains wide (5 chains on either side of the road) has been found to be very satisfactory. In the steeper country and denser stands along the westside of the Sierra, it has been found that strips having a total width of more than 5 chains (2½ chains on each side of the road) are not feasible except in a very few cases.

Two men and a motor vehicle (preferably a pickup truck with open seat in the back for the spotter) make up the crew and equipment for roadside strip surveys under these instructions. One man drives and records the mileage; the other spots the trees. Special forms are used for recording distance, position of infested trees along the strip, and loss data.

Although this method of survey is sound in theory and can be used to advantage by well-trained men, it has a number of practical disadvantages, and the data may be subject to considerable error. Roads may not traverse a fully representative section of the timbered area. They are often located along streams or ridges; they may be used as sheep and cattle driveways; and the frequency of woodcutting or other disturbances along roads often subjects road-strip samples to bias and error.

A test of the road-strip method and several other methods commonly used in estimating bark beetle loss was carried out by P. C. Johnson, W. J. Buckhorn, J. M. Whiteside, and F. P. Keen in 1942 on two large forest areas in southeastern Oregon. The other methods were: (1) estimating by viewing an area from roads and high points without sampling; (2) estimating by viewing plus a few 320-acre cruised check plots; (3) estimating from the 320-acre check plots data (in the office only) by comparing current year's loss with loss from previous years when the check plots and a large part of each area had been cruised for control work; and (4) estimates based on 20-acre line plots surveyed by foot along section lines. Estimates by each method were as follows:

Method and estimator:	*Beetle-killed trees*	
	Embody Unit—57,000 acres (number)	*Silver Creek Unit—71,000 acres (number)*
Observations only—no samples:		
Buckhorn	5, 125	3, 950
Whiteside	4, 730	5, 035
Observations plus 320-acre check plots:		
Buckhorn	4, 150	3, 675
Whiteside	5, 010	4, 735
320-acre check plots—no field observations, Keen	4, 000	3, 400
Line plots—20-acre samples	4, 900	6, 400
Average of 4 standard methods	4, 652	4, 532
Road-strip sampling method	2, 400	2, 730

The estimates were all reasonably close except for those from the road-strip method, which were only about half as large as the others. A 100-percent inventory of loss on the units was not available for a positive check of accuracy. However, as the other methods all checked closely with each other and had proved reliable in the past, it could be reasonably assumed that the estimates by the road-strip method were low.

Aerial Methods in Forest Insect Surveys

The development of forest mapping and observation by airplane brought the possibility that these aerial methods might be adapted to bark beetle surveys. It was thought that they would speed the coverage of large forested areas and provide quick, efficient, and dependable ways of estimating current infestations. Two general fields of use were considered: (1) general reconnaissance, viewing, and strip counts, and (2) sampling of loss through photogrammetric methods. The possibilities were recognized for many years, but the development of aerial survey techniques for western pine beetle surveys progressed very slowly until after World War II.

Miller (*U192*) made the earliest attempt to survey western pine beetle damage from the air in May 1925. Flights were made over Sierra National Forest, Calif., in a photographic-observation plane supplied by the 15th Photo Section of the Army Air Service. Aerial photographs were taken of the Cascadel and Bass Lake units from an elevation of about 9,000 feet above ground. The aerial camera was equipped with a 12-inch focal length lens, panchromatic film, and a "G" filter; exposures were made at 1/50 second or less.

Individual trees could be distinguished on the photographs, but it was not always possible to differentiate between green trees and those killed by bark beetles, particularly those that had advanced to the dark red color phase. A ground check showed that 90 percent of the insect-killed trees retaining discolored foilage registered in the photographs. Trees with a heavy cone crop or needle cast fungus often registered as insect-infested "white tops." Recently infested trees could not be differentiated from recently abandoned ones. The scale of these pictures was too small to be satisfactory, and without a ground check it would have been impossible to estimate reliably the number of dead trees from the photographs alone.

A test was made in 1926 of aerial spotting and sample-plot photographs under eastside conditions. Through arrangements with the Forest Service, a forest fire patrol plane was assigned to Modoc National Forest for a 2-day flight over the Happy Camp-Lava Beds area. Flights were made on September 26 and 28, 1927, over a typical 40-acre plot of infested ponderosa pine forest marked on the ground by white crosses at the corners. Captain Boggs piloted the plane and Keen (*U140*, *U141*) made the observations and took vertical and oblique photographs with a 4 x 5 aerial hand camera held over the side of the open cockpit. Twenty-four pictures were taken, using panchromatic film, "G" and "X–2" filters, and exposures of 1/120 to 1/155 of a second. The "G" filter gave the best contrast in the yellow beetle-killed trees.

This test showed that spotting and plot sampling from the air had definite possibilities and also limitations. Although valuable for general reconnaissance of unfamiliar areas, spotting and counts were impractical in large areas of unbroken forest. Sampling by vertical photographs was shown to be entirely practical for "red-top" surveys, but additional tests were needed to work out many details such as the most satisfactory height of flight, map scale, comparison with ground conditions, and relative cost.

Later attempts to establish loss estimates by spotting beetle-killed trees from Forest Service patrol planes were made by Miller and Salman in 1931 on Tahoe National Forest and by Struble and Munhall in 1941 on Sierra National Forest. Eaton (*U56*), reviewing forest insect air surveys before 1942, stated that the reconnaissance by Miller and Salman was quite unsatisfactory because of rough air conditions, poor visibility, and lack of familiarity of the observers with the terrain. Regarding the air reconnaissance by Struble and Munhall, he said:

> The flight was made at an elevation of about 2,000 feet above the average ground level. One observer tallied the trees that could be seen and the other spotted the trees on a map. A comparison of the two methods showed that one observer had seen half again as many trees as the other. In spite of good visibility, ability to maintain the desired elevation, and good working conditions, the speed of the plane (80–90 miles per hour) was too great to be satisfactory.

Eaton's comprehensive review in 1942 showed the possibilities and limitations of different aerial methods and proposed research to develop sound survey techniques. Eaton also reviewed the work with autogiros in gypsy moth and Dutch elm disease control and discussed the recent photographic equipment and processes that might be adapted to forest insect surveys.

After World War II, the airplane demonstrated its value in reconnaissance or detection surveys of large forest areas, especially for determining whether outbreaks were developing, where they were located, and something as to their general intensity. Airplanes soon became an integral part of the yearly forest insect survey reconnaissance program.

For aerial surveys of western pine beetle infestations, the problems were not how to "detect" infestations, since it was known that all ponderosa pine forests were to some degree infested, but how to sample or measure the intensity of infestations on specific areas. Beginning in 1947, an airplane was based at the Portland Forest Insect Laboratory for use in developing aerial survey techniques and in standardizing procedures. A study was started along three lines: (1) aerial sketch mapping, (2) aerial strip counts, and (3) aerial photography (*U316*).

Aerial sketch mapping applies largely to the delineation of the boundaries and the intensity of defoliator outbreaks and bark beetle outbreaks that kill timber in groups large enough to be outlined from the air. Since western pine beetle infestations are characteristically scattered more or less uniformly over extensive forest areas,

some form of sampling is needed to determine their intensity. Therefore, aerial strip counts or the photographing of sample plots proved more suitable than sketch mapping for western pine beetle surveys.

Aerial strip counts can be used for obtaining quantitative estimates of scattered bark beetle infestations. By this method, a "red-top" tree count is made by observation through a window or an opening in the floor of the plane. The width of strip can be pre-determined by adjusting the size of the opening, the eye distance above it, and the height of flight above ground. Distance along the strip is determined by air speed and time, adjusted by recording the time of flight between two points of known distance on the ground. In the first trials, the hole width was set at 13½ inches, the eye level at 40 inches above it, and the altitude above the ground at 980 feet; these specifications permitted the viewing of a strip 330 feet wide.

Flying at this exact altitude above rolling topography and keeping the plane flying level were among the difficulties encountered. Variations in flight requirements caused variations in the width of strip viewed. Since strip counts can be made only of trees that are visibly colored (either sorrel or red), this method is useful only for "red-top" surveys or counts of past loss. Such surveys do not indicate the extent to which new infestations may be developing in trees still uncolored. Such information can only be obtained through ground checking, which is needed as a supplement to aerial strip counts.

Aerial photography has also been tested with pictures taken at different altitudes and with different films (including color) and filter combinations (*140*). Good weather conditions, bright sunlight, few clouds, comparative calm, and little or no haze are required for satisfactory aerial pictures. Owing to the length of shadows, photography at latitude 45° is limited to the period May 15 to September 15 and between the hours of 11 a.m. and 2 p.m. The experimental work on aerial photographic sampling of western pine beetle infestations indicates that panchromatic film with the G or K-1 filters and at a scale of 1/2,500 is most suitable for sample-plot work. A smaller scale is needed if extensive areas are to be photographed.

Although this research has not yet developed the final solution in sampling bark beetle infestations, it does show definite promise. Aerial photography is probably destined to play an increasingly important role, both in making forest insect surveys and in planning and conducting control measures.

Spotting infested ponderosa and sugar pines from a helicopter was first tried in the spring of 1950 on the 11,200-acre Fence Meadow control project on Sierra National Forest, Calif., where rugged terrain and deep snows made spotting on the ground difficult and costly. On a 4-inch-to-the-mile detailed map of the area, infested trees were spotted from a helicopter during flight at a speed between 30 and 35 miles per hour and at a height of 100 to 200 feet above the forest canopy. Familiarity with the area and good visibility were essential to the accuracy of the survey.

The spotting by helicopter saved unnecessary groundwork, but as Struble (*U312*) pointed out, there were a number of obstacles to be overcome before general use could be made of the helicopter as a spotting tool. One thing needed was a more powerful machine, one

that could fly more slowly or hover if need be. It was found, however, that the helicopter had definite possibilities for use in bark beetle surveys and in spotting for control projects.

The possibilities for bark beetle surveys by aerial methods have barely been explored. With lighter-than-air equipment such as the blimp, maintaining relatively slow and stable speeds, the conditions for accurate observations might be greatly improved. With the perfection of color photography, which can detect the color phases of infested trees, sample plot surveys from the air should become entirely feasible. It can be expected that aerial work will be a very useful phase of forest-insect surveys in the future.

Factors Affecting Loss Estimates Based on Survey Data

The data obtained from bark beetle surveys require interpretation before they can be translated into loss estimates. Several variables must be considered, and this need has prompted much study to improve the reliability and accuracy of area estimates, particularly those based on check plots.

Seasonal Progress of Evident Loss

One of the usual objectives in a plot survey is to find and measure all of the currently infested trees on the sample area to provide a basis for estimating the year's total loss. A second objective is to record as much of the past loss as is needed for a satisfactory analysis of loss trends. The first objective is rarely, if ever, accomplished because there are always a number of the recently attacked trees (varying with season and time of survey) which are not found. Also, if the survey is made in midsummer or early fall, many of the trees that will be killed that year have not yet been attacked. Such trees are therefore missed by spotters and can only be found on later examinations after all the trees have been attacked and have faded.

In 1931 Keen (*U146*) summarized the accumulated survey records from 106 check plots in the eastside type of southern Oregon and northern California to determine how closely these examinations had come to finding the total seasonal loss. The plots could not all be cruised at the same time, so the examinations were spread throughout the season from early summer until late fall. As the same plots were cruised year after year, trees missed one season were picked up the following year. From these data, Keen constructed two charts, one showing "Percent of total annual loss spotted on any date" (fig. 51), and the other "Percent of total winter loss spotted on any date" (fig. 52).

The curves plotted on these charts were shown as straight lines, because it was felt that the variability in loss did not justify a curvilinear relationship. Two methods for using these charts in estimating total seasonsal loss were offered: (1) Add the percentage missed as shown by figure 53 to the visible loss found at the time of the cruise, or (2) if the survey was made after September 1, add the volume of summer generation already spotted to the esti-

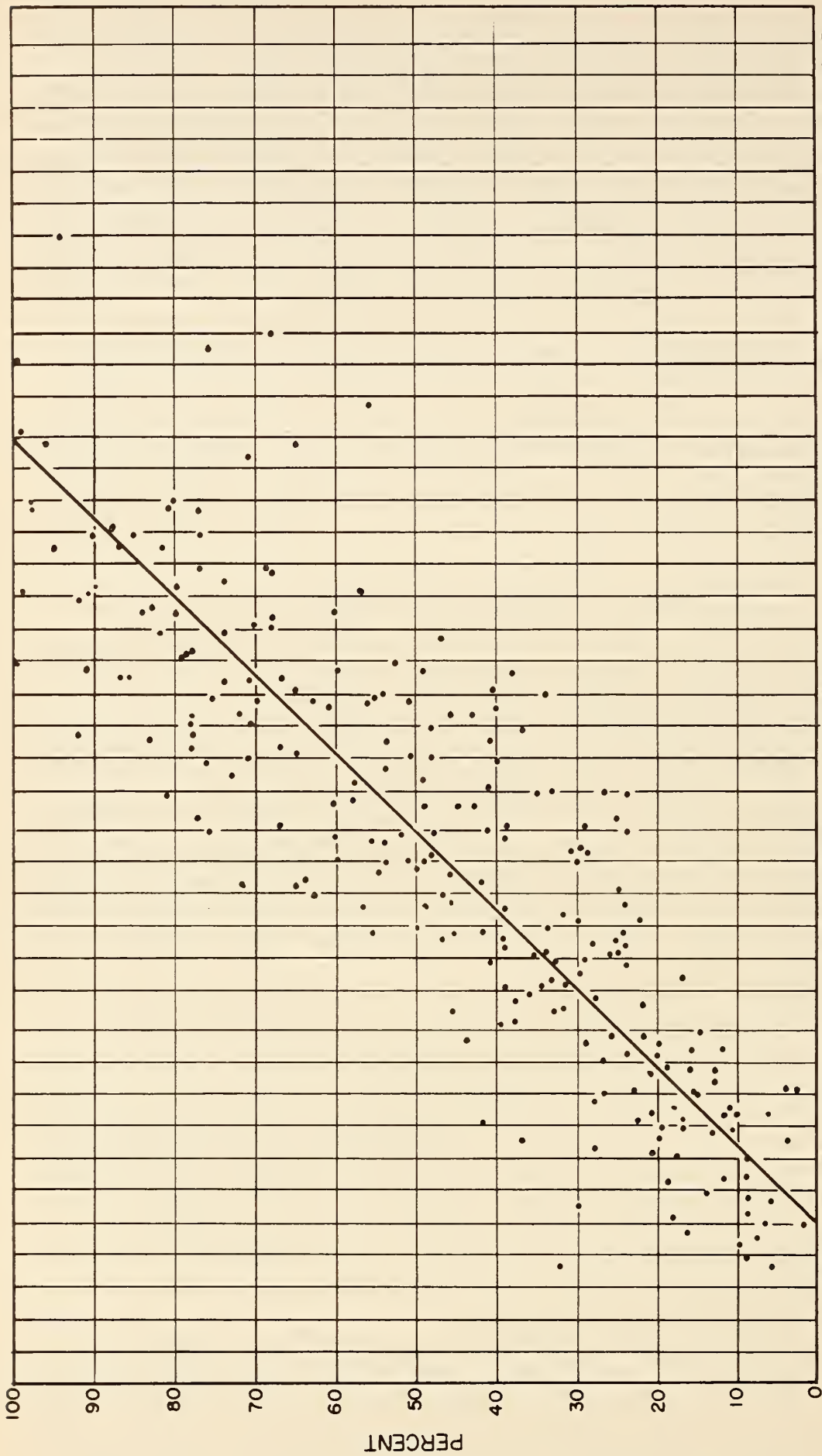


FIGURE 51.—Percent of total annual loss spotted on any date, western pine beetle infestations, ponderosa pine type, Klamath Basin, Oreg., 1923–29.

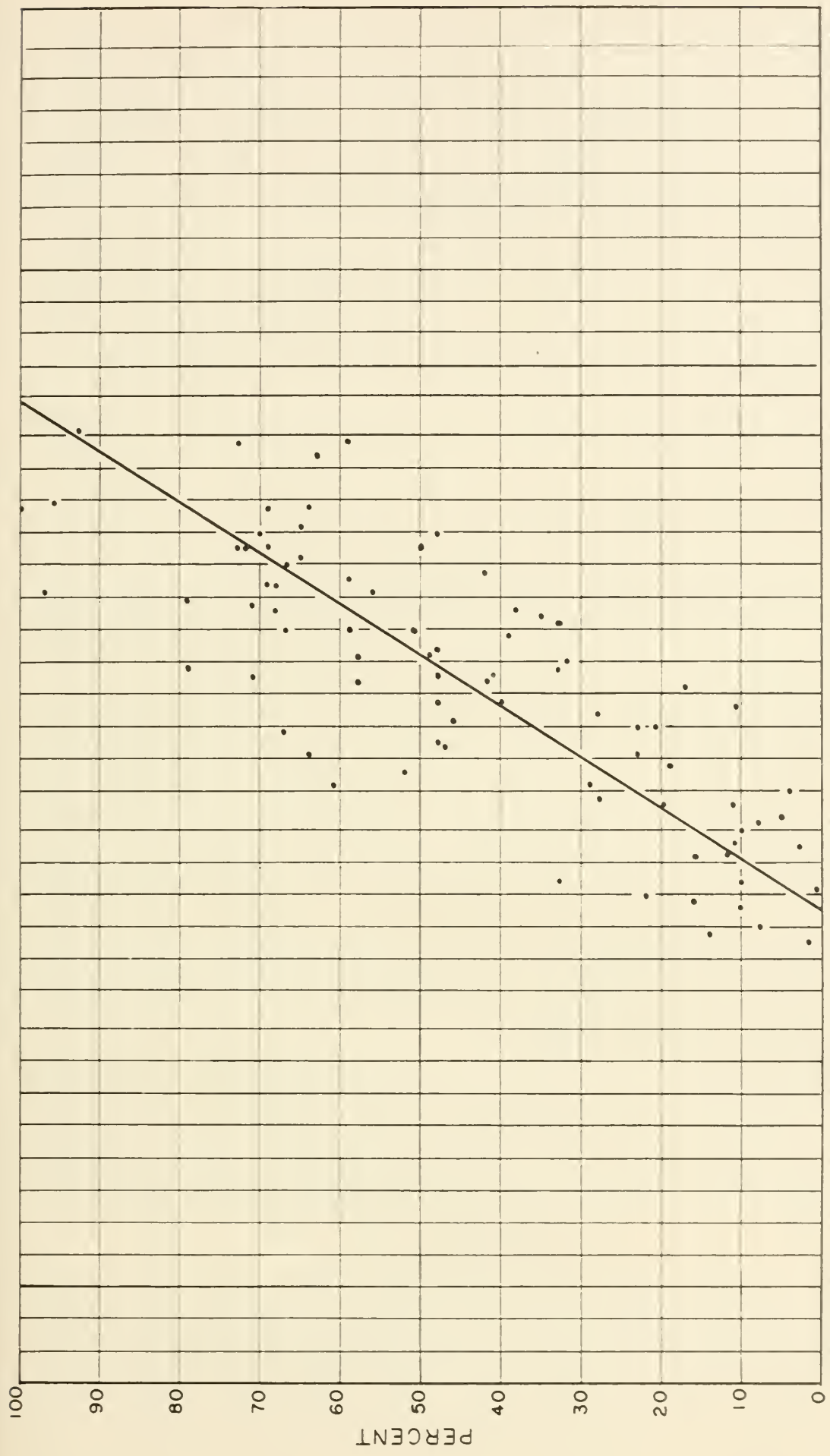


FIGURE 52.—Percent of total winter loss spotted on any date, western pine beetle infestations, eastside ponderosa pine type, Klamath Basin, Oreg., 1923–29.

mated total volume of winter generation trees as shown by figure 52. Keen states:

> In practice the two methods give about equal results. Method 1 tends to overestimate slightly (+ .9 percent average) and Method 2 to underestimate (— .3 percent average). Method 1 is somewhat more reliable, having a standard deviation of 16.8 percent, while Method 2 has a standard deviation of 18.0 percent.

In 1935 Johnson (*U123*) made a similar study using the sample plot records from the California surveys of 1926–33. Johnson prepared separate curves for Modoc National Forest, Lassen National Forest, and the westside Sierra subregion; and for different trees, principal insects attacking, and high and low elevations (fig. 53). He recognized that his curves were supported by limited data, but decided that the flattening of the curves at the beginning and ending of the summer and fall period gave a better estimate than a straight-line relation.

In 1941 Grant (*U75*) added to the work of Keen and Johnson a study of the eastside plot records accumulated up to 1940. He constructed "a new curve for predicting the annual loss from partial loss data taken during the active period from June 1 to December 20 from a statistical analysis of 1,153 observations on sample plots cruised in the ponderosa pine region of eastern Oregon and Washington during the 17-year period, 1923 to 1939" (fig. 54).

The original data all defined curvilinearity; hence straight line regression equations were first computed and then corrected to conform more closely to the data. This procedure was carried out for four subregions—Washington, Blue Mountains, Deschutes, and Klamath Basin—then combined for the eastern Oregon and Washington region as a whole. This new curve was expected to give a better basis for estimating total annual loss than others previously used.

Grant also compared his new Region Six estimating curve with the curve derived by Keen for Klamath Basin, 1923–29; with Grant's Klamath Basin curve, 1931–39; and with Johnson's curve for Modoc National Forest, 1926–33 (fig. 55).

According to Grant (*U75*), the subregional differences in Oregon and Washington are of minor significance: "Differences in the four principal subregions were tested and while slight improvement in estimates was indicated, this was not sufficiently great to justify the inconveniences of using four local curves in place of one regional curve."

Elevation

Johnson (*U123*) compared the curves for ponderosa pine for the higher and lower elevations in the westside Sierra subregions and the different elevations represented by the Modoc and Lassen areas:

> In general losses occurring at higher elevations appear later in the season and terminate earlier than at lower elevations. The northern forests are fairly uniform in topography and elevation and no correction factor is necessary. It becomes important, however, in the westside region due to ruggedness of the country and rapid changes in elevation.

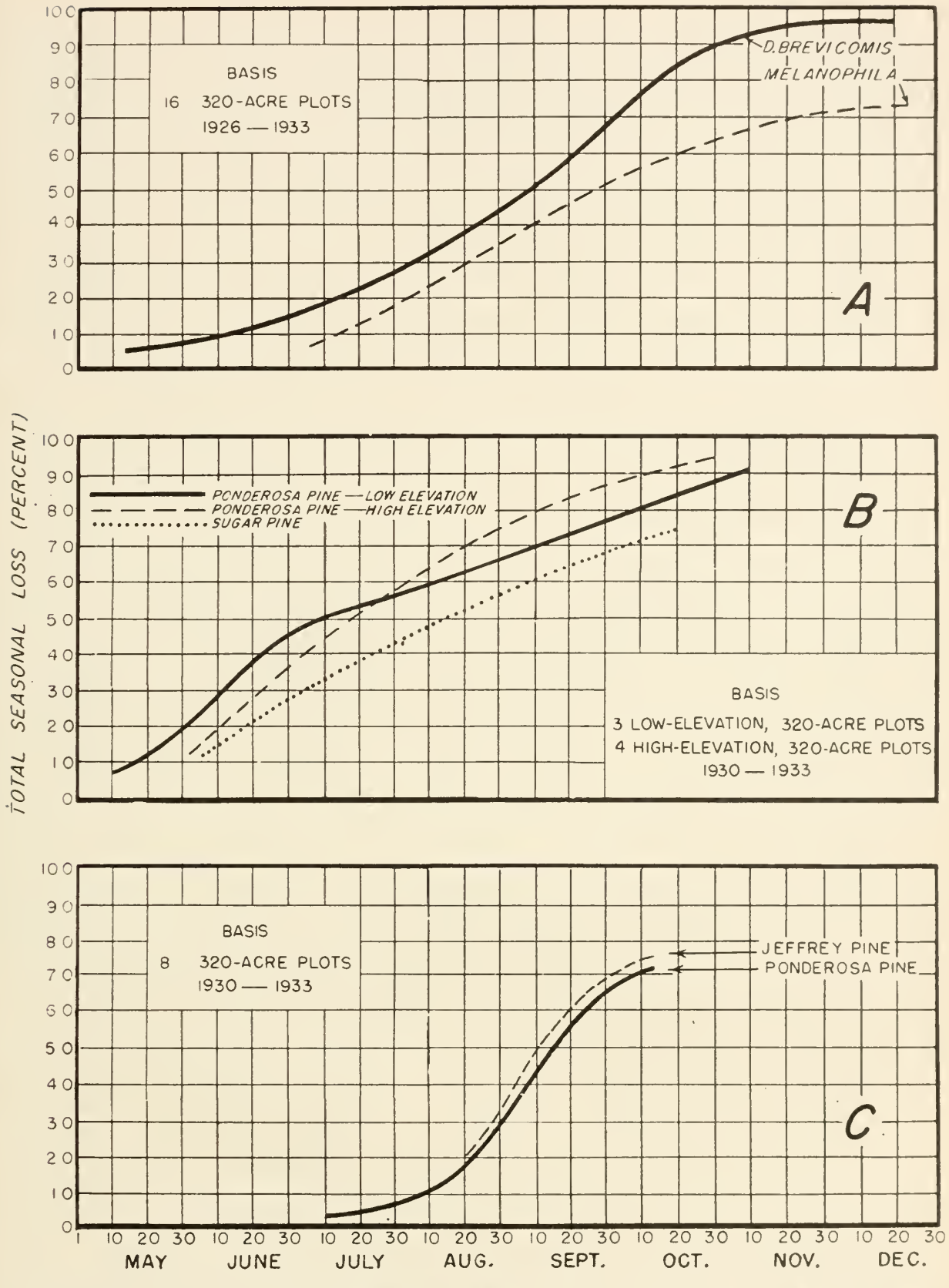


FIGURE 53.—Percent of total seasonal loss cruised on any date: *A*, western pine beetle (*Dendroctonus brevicomis* Lec.) and flat-headed borers (*Melanophila* spp.) in ponderosa pine, Modoc National Forest, Calif.; *B*, all primary insects in ponderosa and sugar pine, westside Sierra subregion, Calif.; *C*, all primary insects in ponderosa and Jeffrey pine, Lassen National Forest, Calif.

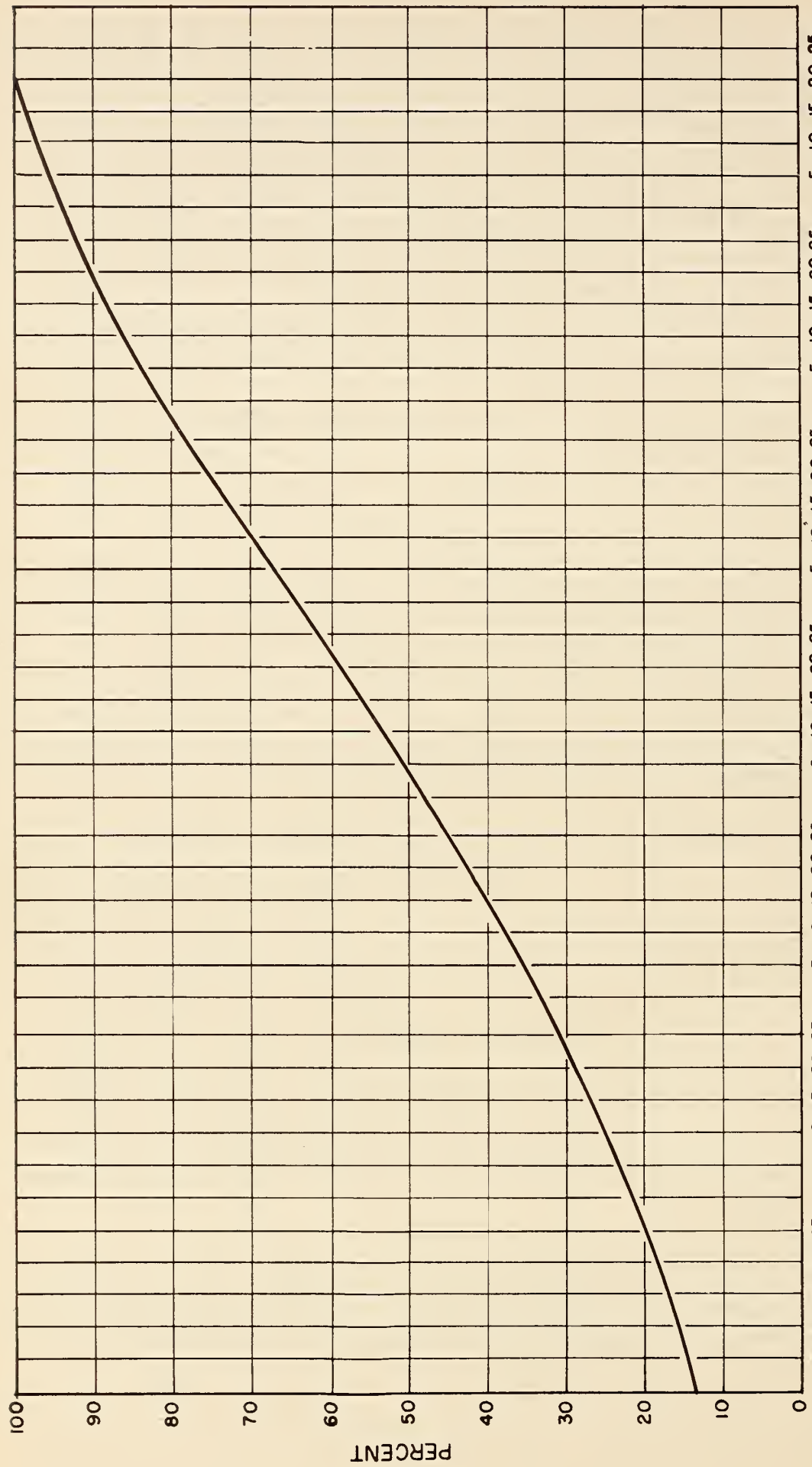


FIGURE 54.—Percent of total annual loss spotted on any date. Eastern Oregon and Washington, 1923–39. Curve statistically derived from 1,153 observations.

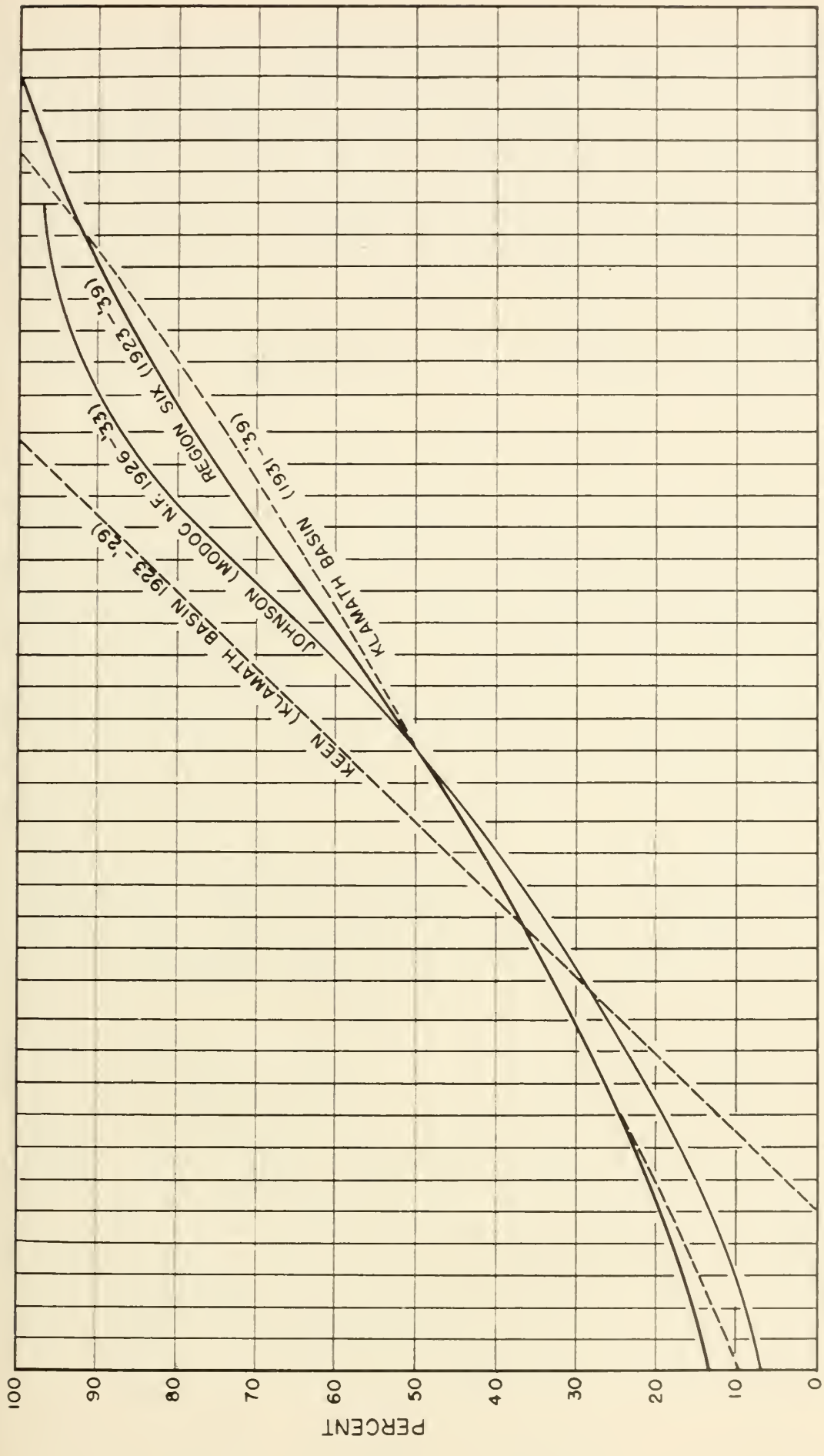


Figure 55.—Percent of total annual loss spotted on any date. Comparison of studies showing effectiveness of spotting western pine beetle infestations, eastside ponderosa pine type.

Composition of Stand

Johnson (*U123*) also considered that the mixture of species in a pine stand may be a factor in modifying loss estimates:

> The time and rate of development of the losses throughout any one season may vary according to the pine species present, their proportion in the stand, and the primary insect attacking them. Jeffrey pine losses on the Lassen developed throughout the average season at practically the same rate as those in ponderosa pine. On the other hand, sugar pine and ponderosa pine losses on the west-side of the Sierra presented different rates of development of seasonal losses. Any estimations made of total seasonal losses would, therefore, be the result of two separate estimations; one for sugar pine and one for ponderosa pine.

Trend of Infestation

Keen, Johnson, and Grant all recognized that sudden changes in infestation trend during the flight period and after the annual survey can throw the seasonal estimate off considerably. Such changes can make the estimate either too high or too low, depending upon whether the infestation rises or falls. In either case, direct control plans may be drastically affected. According to Keen (*U146*):

> If the infestation trend changes very markedly between summer and winter brood, the total estimated loss on incomplete data may be somewhat in error, especially if the estimate is based on records taken early in the summer.

However, this error has not been as large as might be supposed. Johnson (*U123*) states:

> A sudden increase during or following the survey will normally result in estimating the total seasonal losses too low. To offset this, the percent figure read from the curve for the date of survey must be decreased according to the judgment of the estimator.

Grant (*U75*) discusses this phase more fully:

> As a general rule total annual loss is apt to be underestimated during periods of increasing beetle activity, but this is dependent on the season during which the estimate is made. Epidemics usually progress irregularly and total annual loss is difficult to estimate during early season spotting. It is quite possible that estimates made from a normal curve may be low during the early part of the season and high at the end or vice versa. In such cases the errors of estimate may be compensated for the year. A knowledge of the effects caused by sudden changes in the infestation and the trend of an epidemic should be more helpful to the estimator during epidemics than estimating coefficients read from a normal curve of total loss spotted on any date.

Seasonal Variations

According to Keen (*U146*):

> In some years when spring comes early and the autumns are late, the period of activity is very long. In other years with late cold spring and a short summer, it has been noticed that attacks are

completed much earlier than usual. In such case a much higher percentage of the total loss will be found on any given date than in years when the attack period extends later into the fall. This was particularly noticeable in 1927 when the use of the estimating graph gave an overestimate of approximately 14 percent.

These seasonal variations result in a rather wide spread between years in the date when any certain percentage of the infestation can be spotted. This is shown in table form in Keen's report and by comparative curves in the reports by Johnson and Grant.

Author:	*Region*	*Period*	*Spread between dates when 50 percent of infestation was spotted*
Keen	Klamath Basin	1923–29	Aug. 10 to Sept. 9.
Grant	Klamath Subregion	1923–39	Aug. 15 to Oct. 15.
Johnson	Modoc National Forest	1926–33	Aug. 25 to Oct. 10.

Keen also found a relationship between the number of clear days and the loss estimate. The number of clear days in a year is a rough measure of temperature and length of active season for brood development. A large number of clear days means more than average brood development, greater than average loss, and hence an underestimate of beetle damage. Conversely, any factor that retards beetle activity results in an overestimate of annual loss. Grant (*U75*) states:

> As a general rule it may be stated that any climatic factor which increases the resistance of trees to beetle attack or retards beetle activity will result in an overestimate of total annual loss. Losses are overestimated to some extent when the active season is preceded by very low winter temperatures.

Summing up the effects of seasonal variations, Grant says:

> Annual variation is largely a function of climatic changes and beetle trends, and no correction for these is proposed other than the entomologist's ability to predict the effect of weather and trend of beetle activity from his general observations and past experience.

Errors Related to Time of Cruise

Keen (*U146*) analyzed the Klamath Basin data to see when the surveys should be timed to give the most reliable estimates:

Time of estimates:	*Standard deviation of estimate on any one section (percent of error)*	*Standard error of estimate for an average of 12 sections (percent of error)*
July	81.4	23.5
August	33.0	9.5
September	21.4	6.2
Any time after Sept. 1	17.5	5.0
October	13.8	4.0

Keen's conclusions:

> Estimates made on the basis of early attacks in July will necessarily be very inaccurate. Obviously the accuracy of estimates will improve during the late summer and fall as a higher percentage of total attacks will be evident . . . It is safe to assume that

with a three-man crew after the first of November about 90 percent of the trees will be found if the work is carefully done.

From the Oregon and Washington records, Grant (*U75*) found that:

> Spotting has been done generally during August and September on pine beetle surveys, and these conditions, as far as estimating total loss is concerned, favor the present practice of making midseason surveys; namely, the strength of the estimating curve during this period, the small annual variation, and the small subregional variation during midseason.

Errors Due to the Personal Factor

Keen (*U146*) states that:

> . . . considerable variation in results will be due to the experience, interest, carefulness, and accuracy of the individual spotters. It has been found that where one man will actually find 99 percent of the infestation evident on an area, another will find only 75 percent.
>
> . . . In the long run, it may be assumed that two spotters of equal ability will mark the same number of trees, or that each spotter will mark half of the total on any section. From the cruises of 106 sections it has been determined that the standard deviation of marking for any one spotter is plus or minus 20 percent.

Johnson (*U123*) states that:

> Experience has shown that the efficiency of the average spotter varies with such conditions as (1) training and experience, (2) time of year, (3) speed with which work is pushed, (4) topography and type of infestation, (5) weather conditions, (6) general morale of the men due to living conditions, personality, and willingness to cooperate. Personal errors in spotting will probably always occur, but should be kept to a minimum by the use of experienced men, careful selection and training of new men, and proper supervision of the work.

Errors Due to Methods of Cruising

Keen (*U146*) states:

> The intensity of the cruise will make considerable difference. The width of strip, the number of men in a crew, and the rapidity with which the ground is covered are all factors affecting the final result. In one case, a 3-man crew using 10-chain strips (5 chains per spotter) picked up 50 percent more trees than were found on the same area by a 5-man crew taking a 20-chain strip (5 chains per spotter). With the larger crew, the tendency was to bunch around the compassman and leave the outer strip poorly covered. In another case during fall cruising, a 5-man crew using 2½-chain strips obtained 17.8 percent more trees than would normally have been found by a 3-man crew at that time of year.

Methods of Bark Beetle Hazard Surveys

Methods used in bark beetle hazard surveys are at best preliminary —still on trial. The soundness of any method used for this purpose is dependent upon an estimator's understanding of factors that contribute to the hazard of bark beetle attack in pine stands and upon his ability to recognize and appraise these factors. These basic factors are still under investigation: the work that has been done to date on this phase of beetle hazards is reviewed in Section III and under "Hazard Zonation" in Section IV, p. 242. So far, no method of hazard zonation can be considered as final or standardized.

Spotting for Control

The methods used for "spotting"—that is, locating, tagging, and mapping infested trees to be cut and treated in control work—are essentially the same as those used in intensive survey work. The primary differences are that in spotting all infested trees are visited and marked, different records are taken, and all of the acreage to be treated is covered instead of just a sample. Two principal methods have been used: (1) the topographic method, and (2) the strip method. Spotting is one of the most important phases of control work, because success depends largely upon finding a high percentage of the infested trees (*61*).

Topographic Spotting

The topographic method is adapted to country with steep and well-defined drainages. It is best handled by one man working alone. The spotter usually lays out a definite drainage to be covered each day, then follows the ridges or the contours and works back and forth along the slopes. He marks all of the infested trees and plots them on a map; thus he finds a good topographic map and a pair of fieldglasses invaluable aids to his work.

The topographic method has the disadvantage of not covering an area in a uniform manner; without question, some trees are missed. It has the advantage, however, of being less expensive than other methods and is particularly well adapted to rough country.

Strip Spotting

The strip method of spotting is primarily adapted to flat or gently rolling country or to dense forests that cannot be viewed from a distance. Because it is systematic, strip spotting is usually more efficient than the topographic method. The advantages are: (1) thorough and uniform spotting of an entire area, and (2) accurate mapping of the infested trees. These features are important in control operations to avoid loss of time by treating crews in relocating infested trees.

Strip spotting is best handled by a three-man crew, one compassman and two spotters. The compassman carries a line with compass and determines distance by pacing. He plots infested trees as they

are referred to him by the spotters, and maps topographic and cultural features of the area covered. The spotters work in a strip on either side of the compassman, marking and tallying all infested trees that require treatment.

The width of strip depends upon the density of the timber stand and the intensity of the infestation. In fairly open stands of ponderosa pine, a 5-chain strip can be covered satisfactorily by each spotter. Although strip spotting has been done by crews varying from one to five men, the three-man crew is advocated and most commonly used for spotting in western pine beetle infestations (fig. 56).

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FIGURE 56.—A spotting crew at work on a western pine beetle control project.

When a spotter finds an infested tree, he makes conspicuous blazes on at least two sides and marks a serial number on the blaze. Sometimes he tags the tree with a card or a strip of cloth so it can easily be found by the treating crew. And he records the tree on a "spotting" tally sheet giving diameter and other information. The tree and serial number are also plotted on the compassman's map, copies of which are furnished the treating crews so that the infested trees can be located and treated.

The amount of country that can be covered by a spotting crew in one day is governed largely by the number of infested trees that have to be marked on each section, the character of the topography, the amount of detail to be recorded, and the method of marking each tree. In western pine beetle infestations ranging from 50 to 250 trees per section, a 3-man crew can spot from 25 to 125 trees on 320 acres per day. On areas running less than 40 trees per section, and with gently rolling topography and little brush, as much as 480 to 640 acres may be covered in a day. With infestations heavier than 250 trees per section, less than 320 acres can be covered.

Spotting, essential to any control project, is usually handled as a part of the project operation. The spotters are under the administrative jurisdiction of a control supervisor and under the technical direction of an entomologist, who designates the methods to be followed and inspects the types of trees marked for treatment.

PLANNING AND REPORTING BARK BEETLE SURVEYS

Survey Planning

Bark beetle surveys covering large areas usually find a wide variation in forest conditions, infestation types, climatic influences, and land ownerships. In order to cover such areas effectively, it is necessary first to decide how data will be collected and what methods of survey will be used. The coverage must be planned either before or during the progress of the survey, and infestation units of advantage in summarizing survey data and in making control recommendations must be established.

It is highly important that the organization and initial planning of surveys be carefully and intelligently done, especially for permanent survey programs that are to be continued year after year. Later changes in area organization or methods of coverage can break up continuity of records and interfere with the interpretation of long-term trends. Manuals have focused attention on techniques but have largely bypassed discussion of the overall planning of bark beetle surveys. However, underlying much of the work included in the studies of the Lamb's Mine unit (*133*), the Rogue River survey (*U178, U181 U221*), and other earlier surveys was the attempt to develop the best methods of area coverage and to determine the components of a satisfactory unit for survey and control purposes.

Selection of Survey Methods

The selection of survey methods is inevitably influenced by (1) the purpose, desired accuracy, and intensity of the data to be collected and (2) the physical conditions of topography and forest types in the area. In a very generalized way, these considerations can be outlined as follows:

1. Preliminary appraisals of conditions; rough estimates.—Topographic method or road strips without measured check plots.
2. Loss estimates of reasonable accuracy for control or management purposes.
   a. Rough country, broken types.—Examination and measurement of trees along trails or contour strips, supplemented by topographic survey of entire area.
   b. Rolling country, continuous type.—Measured check plots, supplemented by road-strip counts or topographic surveys.
   c. Flat country, not easily viewed.—Measured check plots supplemented by reconnaissance and road-strip counts.
3. Accurate loss data on specific areas for research purposes.—Measured check plots, usually of permanent location, often with trees tagged with serial numbers.

Many reporting areas have been found to contain such great variations in conditions that a combination of all methods has been used to arrive at loss estimates. On the whole, no hard and fast rule has been prescribed for the selection of methods, and the last court of decision always has been the judgment of the estimator as to the method best adapted to the purposes of his survey and to the area he is to cover.

Area Subdivisions and Terminology

It has been common practice to recognize land divisions such as national forests, Indian reservations, national parks, or timbered areas protected by private owners or under State control as survey areas. In such areas, beetle infestations can be treated as common problems affecting all ownerships. But for convenience, the survey area (or general report area) is broken down into smaller units in which infestation conditions can be summarized and analyzed separately.

The indiscriminate use of terms to designate the types of areas used in bark beetle surveys led to a canvass of Federal forest entomologists in March 1944. From the results of this canvass, a uniform set of terms and their definitions was to be used as a guide for the organization of survey areas.

Natural Divisions

Natural divisions delineate a forest along geographical, topographical, and ecological lines. Boundaries follow natural divides, such as ridges, rivers, and openings.

Regions.—Major ecological divisions, such as the ponderosa pine region, the Douglas-fir region, and the redwood region.

Subregions.—Major geographical subdivisions of the region, such as west Sierra, northeastern California, Klamath, Deschutes, and Blue Mountain.

Divisions.—Major geographical subdivisions of the subregions, such as southern Sierra and upper Deschutes. (This category has only a limited usefulness.)

Areas.—Groups of geographically associated units within a division of the subregion; a natural block including several closely related units. (This roughly conforms to a working circle.)

Units.—The smallest divisions of a forested area, based upon entomological considerations; the smallest territories that would have to be considered if control were undertaken.

Administrative Divisions

Divisions of a forest along administrative lines are based upon who manages and protects the area.

Region.—(U. S. Forest Service Region 5, Region 6, etc.)

Forests.—National forests, Indian reservations, national parks, or large tracts of private land administered by one agency. (These are generally used as reporting areas.)

District or "reporting district."—A ranger district or other subdivision of a forest forming an administrative entity. A block of land comprising an arbitrary but convenient reporting area. (Used mainly in annual reports by forest officers.)

Political Divisions

Finally, some areas are divided along recognized political lines—*State*, *county*, *township*, *range*, and *section*.

Each of the major divisions is completely independent; only occasionally do the lines of one coincide with the lines of another (e.g., when county or national forest boundaries follow the crest of a mountain range). Therefore, natural units and areas seldom conform to administrative or political boundaries.

The Infestation Unit

The first surveys attempted to find an infestation unit that was an entomologically homogeneous area independent of adjoining similar units. Miller (*U184*) defined this conception of the infestation unit in 1920 as follows:

> By infestation unit we mean an area in which the amount of infestation will not be materially increased by beetles flying in from outside areas, or decreased by beetles leaving the unit. In other words it is assumed that the factors which influence the increase or decrease of beetle populations are operative entirely within the unit itself and are not affected by population changes outside the unit. Two factors then must be taken into account in setting up an infestation unit: (1) effective boundaries, and (2) size of the area. For effective boundaries we are forced to rely upon topographic features, such as high ridges or breaks in type which create barriers that the beetles are not expected to cross in flight. Failing to find effective barriers the infestation unit must consist of an area so large that the amount of infestation which may drift across its borders will not materially increase or decrease the total volume of infestation to an extent that will change trends within the unit.

The ideal infestation unit seems to exist only in theory. Insufficient information on flight habits of the western pine beetle makes it uncertain just what sort of barriers will prevent beetles from leaving or entering an area. Also it is not known just how far population movements may extend where there are no barriers. Consequently, the selection of infestation units has been based on compromise with a number of factors, some of which are not entomological at all. Factors considered important in the setting up of infestation units include size of unit, topography, breaks in timber type, and land ownership.

The Size of the Unit

No standard acreage has been adopted for infestation units, and as a rule the size has been determined by other considerations. Because flight distances have not been definitely established, no specific acreage can be chosen as adequate to overcome the flight factor. In

general, units selected in the commercial pine areas have been 10,000 to 50,000 acres. Areas of less than 10,000 acres appear too small and those above 50,000 acres too large for satisfactory survey and control units. Adaptability to administration for control has been one of the most influential factors in consideration of the size of unit.

Topography

In mountainous country, the tendency has been to select tributary drainages of large rivers as infestation units. Where these tributary drainages are bounded at their sources by high divides, often with breaks in the pine type, and are separated from other tributary basins by secondary or lateral ridges, the boundaries were very easily drawn. Such areas have been considered as satisfactory infestation and control units if they included about 10,000 to 15,000 acres of pine type. Where suitable timber basins could not be delineated, canyons have been used as the boundaries, with the timbered ridges or plateaus between them making up the unit. Units of the topographic type are fairly common in the western slopes of the Sierra and Cascades but are found less frequently in the plateau like formations east of the crest.

Breaks in Timber Type

Breaks in timber type may consist of open country or changes in the vegetation cover where pine is not an important element in the composition. These type changes are quite often related to elevation. They may be rocky or barren ridges on divides; fir types on higher elevations; or oak, brush, or desert types at lower elevations. In many areas topography and type changes can both be taken into account in establishing units.

Land Ownership

Ownership has not been given much consideration in establishing infestation units because this factor is unrelated to the behavior of the beetles. However, for purposes of control administration, it is at times expedient to consider land ownership in establishing unit boundaries.

Infestation Areas

A natural block of several closely related units is called an infestation area. Such areas roughly conform to working circles. In the past, they have been established along natural boundary lines. Entomological considerations and convenience in control projects have been the most important factors in considering the boundaries of infestation areas.

The term "reporting areas" has also been used more or less synonymously with infestations areas, except that the emphasis here is on administrative grouping of units rather than natural ecological groups.

Forest management working circles have rarely been used as infestation areas, even though considerable effort has been made to adjust infestation units to the working circle pattern. The problem

is that working circles are usually established entirely on the basis of topography, ownership, and the manner in which the timber will be logged. There has been no reference to entomological considerations such as the proximity of related bodies of timber having similar ecological and infestation characteristics.

However, the use of working circles as infestation areas can be expected to increase as management plans for the commercial pine stands are perfected, especially where sustained-yield units are set up integrating all ownerships under one plan. The advantages of using working circles for infestation areas are as follows:

(1) The boundaries are established for long-term use and are recognized by forest officers.

(2) Stand resources have been or will be inventoried and growth estimates determined, thus providing the necessary data for determining rate of depletion caused by insects.

(3) Data on age and composition of the stand provide a clue to potential bark beetle hazards.

(4) Cutting programs can be modified and shifted so as to reduce the bark beetle hazard and thus act as an indirect control against serious losses.

Reporting of Bark Beetle Surveys

The forms used for survey reports have varied from one page questionnaires to long discussions of all the elements involved in an infestation area. The variations have depended upon the purposes served by the report and the imagination of the author. Attempts have been made by different agencies to standardize report forms, and survey manuals have proposed a number of outlines and forms to be used in survey reporting. Keen (*61*) gives a complete series of outlines for survey and control reports including:

1. Reports of preliminary reconnaissance of infested areas.
2. Annual forest insect reports (for use by district forest rangers).
3. Reports on bark beetle estimation surveys of infested areas (with separate outlines for the first and for subsequent reports).
4. Three outlines for reports on control projects covering work plans, seasonal work, and the results obtained by control.

The main features of the survey report outline (number 3) have been followed in most of the surveys conducted by the Forest Insect Laboratories. The topics covered are as follows: (a) *Introduction.* History of area, objectives of the survey, and methods used. (b) *Survey data.* Conditions in survey area, insects responsible for the losses, character of losses, and estimates by units. (c) *Conclusions and recommendations.*

It is very difficult to fit all surveys into a standard or conventionalized form of report. Great variations exist in conditions in subregions and areas, and in objectives and perspectives of the surveys. The most informative reports appear to be those in which the author has carefully thought out the points that he thinks are the salient features of the survey, grouped these points in logical sequence, and presented them concisely in his own way. Good writing and clear style are as necessary in bark beetle survey reports as they are in any other form of reporting.

SECTION V. CONTROL METHODS AND STRATEGY

DEVELOPMENT OF DIRECT CONTROL TECHNIQUES

The first method proposed for western pine beetle control involved nothing more than the killing of beetle populations. It was considered necessary (1) to find the trees in which the broods were concentrated, and (2) to cut these down and destroy the infested bark by burning. The theory was that beetles so destroyed could not kill any more trees; that if the work were done thoroughly over a large enough area, the amount of timber killed subsequently would be negligible. The long overwintering period when the broods are dormant in infested trees favored this theory. However, the method had disadvantages because the burning charred the logs, and the rapid development of checking, stains, and rots soon rendered most of the treated material unmerchantable (*7*).

Methods for protection of living trees from attack were dismissed for commercial pine forests. Even if repellant or toxic sprays could be developed, it was said, they would have to be applied on such a scale that costs would be out of line with possible benefits. Consequently the strategy of destroying the beetles, rather than protecting the trees from attack, was followed over the long period of years covered by control operations. Only recently has an indirect method for control evolved—the removal of the more susceptible trees from the stand by sanitation-salvage logging (*76*).

Under the strategy of control through reduction of populations, the method that killed the most beetles at the lowest cost was usually the most satisfactory. One of the first requirements was that the equipment be light enough to be carried around in the forest, and that the techniques be simple enough to be mastered in a short time by the type of labor available in forest and lumbering communities. Many methods for killing beetles have been proposed and developed, and the selection of any particular method is usually governed by the conditions where it is used, e.g. costs, ground cover, fire hazard, and effectiveness of the method against the type of infestation encountered. Although only a few methods have proved to be practical, this review takes up all that have been tested in order that the record of trial and error may be complete (*25*).

Fell-Peel-Burn

Fell-peel-burn was the first control method and the one most frequently used on western pine beetle projects. Nothing has yet been found that will kill beetles as effectively and as cheaply as fire. Hopkins (*44*) briefly describes this method, as applied against the western pine beetle and species of similar habits:

> Removing the infested bark, and burning or otherwise destroying it, is necessary to kill the developed broods of larvae, pupae, and adults which may be located in the outer bark. . . . The time to

do the work . . . is from the time activity ceases in the fall until 2 or 3 weeks before the normal time for the winged adults to begin to emerge and fly.

Specific instructions for the fell-peel-burn method are given by Keen (*61*) in his "Manual of Bark Beetle Control in Western Pine Forests." According to Keen: "This method is applicable to the treatment of any bark beetle infestation, and is the method most widely used . . . on account of its cheapness and its effectiveness in disposing of the beetles and in cleaning up the slash that results from the operation."

Techniques of the fell-peel-burn method were developed with experience. One of the earliest modifications was concerned with the peeling procedure. At first the entire log was peeled (fig. 57), but

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FIGURE 57.—Peeling an infested ponderosa pine log before burning the bark.

on many trees the infested bark adhered so tightly that the peeling process was tedious and time consuming. As a result, attempts were made to treat these tight-barked trees without peeling by piling the limbs and other fuel material over the log to create a very hot fire. This additional heat, however, had very little effect upon the brood on top of the log. The updrafts of the fire and the heat-insulating properties of ponderosa pine bark prevented the production of sufficiently high temperatures to kill the broods. Only along the bottom and lower sides of the log where the fire was banked between log and ground was there an effective kill in the unpeeled bark.

A satisfactory practice was finally perfected. In brief, the method commonly used consists of felling the tree, limbing it, peeling the infested bark only from the top half of the log, and piling the loosened bark along the sides of the log. A fireline is constructed around the felled tree whenever fire is a hazard in the forested area. Then the piled bark is set afire (fig. 58). By the time the bark is completely

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FIGURE 58.—Burning the bark of a ponderosa pine infested with the western pine beetle.

burned, the lower half of the log is charred, but the heartwood usually remains intact.

Effectiveness of the fell-peel-burn method depends to a great extent upon finding and treating all of the infested trees in a control area. Since it is not possible to attain 100-percent spotting efficiency (see Section IV, p. 257), infested trees are often missed on control operations. From these untreated trees, new beetles later emerge to reinfest the area.

Keen made a study of the amount of reinfestation that developed during the first season after control on 29 treated sections on the southern Oregon-northern California project. A rough correlation was found between the number of trees missed in spotting and the amount of new infestation that developed (fig. 59). The most striking feature on the graph is the wide variation in the amount of reinfestation where only 5 to 15 trees per section were missed. Where more than 20 trees were missed, the amount of reinfestation was consistently high. Natural control factors, or the lack of them, undoubtedly account for much of the spread of points shown on the graph.

The cost of control by the fell-peel-burn method depends largely upon labor efficiency. From a study of the southern Oregon-northern California pine beetle control project, Keen determined the minimum, average, and maximum time required by a three-man crew to cut-peel, and burn a given number of board feet of infested timber (fig. 60).

Minor modifications of the fell-peel-burn technique have been developed to fit special conditions of the infested trees and the fire hazard. One common practice is to cut off about 20 feet of the

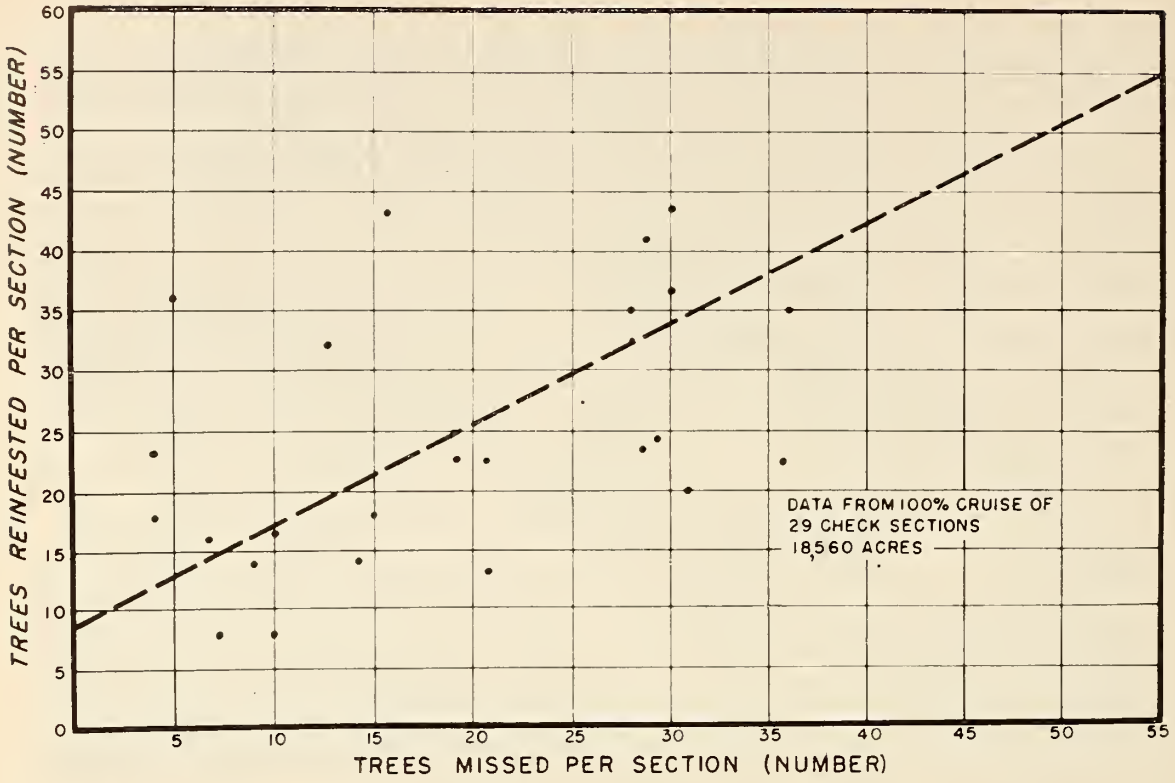

FIGURE 59.—Relation of missed trees to subsequent reinfestation following direct control by the fell-peel-burn method. Southern Oregon-Northern California Pine Beetle Control Project, 1922–23.

top of the trunk, buck it into short lengths that can be handled, and pile these along the main trunk to help bank the fire.

Pit Burning

Dry periods are often encountered during the course of control projects when the bark can be burned only by using extreme care and by taking costly precautions to prevent the spread of fires. It is also desirable at times to conduct control during the summer months. Under these conditions, the practice has occasionally been followed of burning the bark in a pit where the fire can be kept under control. A shallow pit is dug close to the felled tree, and as the bark is peeled a small quantity at a time is burned in the pit. After the burning is completed, a further safety precaution is taken by covering the pit with soil to prevent live coals from blowing into nearby flammable material. Pit burning is slow and expensive and is used only when the fire hazard is extreme.

Decking and Burning

Decking and burning, proposed by Hopkins (*44*), has been practiced at times in connection with the fell-peel-burn method. Where small infested trees are closely grouped, it is often more economical to burn the unpeeled logs in piles than to peel and treat each tree separately. The decking method usually requires some additional fuel material to get the fire started; once the fire is burning, however, the heat is banked under and between the logs and the bark is burned entirely. In the larger decks, the bottom logs are often entirely con-

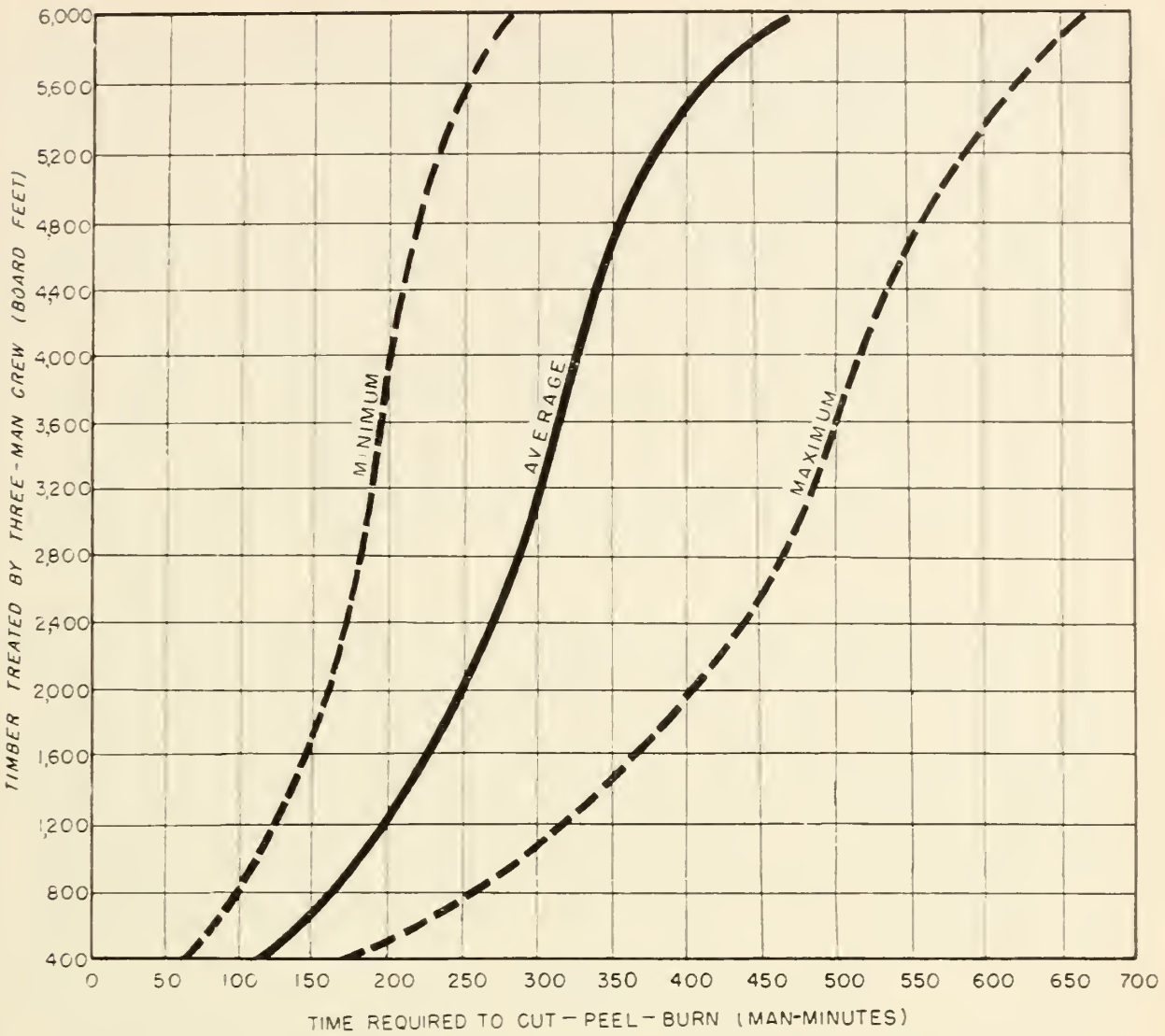

FIGURE 60.—Time required to cut, peel, and burn a given number of board feet of infested timber by a three-man crew.

sumed, and the top logs settling into a bed of coals are either burned or so thoroughly charred that no beetles escape. The decking and burning method is impractical in large timber without power equipment for hauling and piling the larger logs (*U104*). The method necessarily prevents salvage of the treated logs because of the degree to which they are burned.

Use of Fuel Oils in Burning

The first attempt to use oil as an aid in burning the bark on infested trees was made by the Long-Bell Lumber Company on the Antelope Control Project in northern California in 1921 (*U219*). In this test, the bark of a standing infested tree was sprayed with kerosene and immediately fired. Although a liberal amount of kerosene was used and the oil burned fiercely on the surface, the heat did not penetrate the bark deeply enough to kill larval broods. The fire could not be reflected or "banked" against any part of the trunk. The bark itself was charred only where there was an accumulation of resins. The experiment demonstrated that there was little possibility of heating ponderosa pine bark enough to kill bark beetle broods in a standing tree.

In 1932 Chemist Norman Gay of the Standard Oil Research Laboratory tested the possibility that infested bark on felled trees could be burned or heated to temperatures lethal to the broods with the aid of a slower burning fuel oil. Gay (*35*) carried out his experiments in cooperation with the Berkeley laboratory on the sugar pine sale control project on Sierra National Forest. These experiments were well planned; pyrometer readings were kept to determine the degree of heat reached under variable conditions such as position of the bark on the log and the amount and character of fuel used, and accurate cost records were maintained.

It was found that bark on top of the log absorbed very little heat, regardless of the amount of oil used; lethal temperatures were obtained only when enough limbs and solid material were piled over the log to hold the fire for a considerable length of time. On the lower sides of the logs, the bark was easily burned. Gay's conclusions were:

> During periods of low fire hazard when all the limbs and other surrounding brush can be utilized to heat the bark and oil used as a supplementary heating medium, we believe that the use of oil will reduce the costs due to the elimination of the peeling operation.
>
> During periods of high fire hazard when the size of the fire must be kept to a minimum, we believe that peeling the bark is cheaper, due to the fact that all the limbs cannot be utilized to generate heat and an exorbitant amount of oil will be required to effectively burn the bark.

Goop

The success of incendiary materials used in aerial bombing in World War II prompted a further attempt to improve the oil-burning method of control. One of the most effective of these war-developed materials was a mixture known as goop, which became available in surplus for a few years after the war. Goop is a dark gray, puttylike material composed of finely divided magnesium and magnesium impurities, asphalt, and kerosene. It burns with a very hot flame producing temperatures between 2,000° and 3,000° C.

A report by Struble (*U306*) gives the results of tests made in May 1946 in cooperation with the Army and the Permanente Metals Corporation—tests on large, mature, beetle-infested sugar pines and ponderosa pines. In these tests, goop was thinned to a desired consistency for spraying or pouring on logs by mixing it with an equal amount of fuel oil. Effective kill of broods under the bark was obtained by the following techniques:

1. Where the bark was less than ¾ inch thick, goop slurry (50 percent diesel oil) alone was applied to the bark surface and burned.
2. Where the bark thickness was greater than ¾ inch, goop slurry was applied as above but the top of the log was covered with (a) a layer of pine needles overlaid with 4 inches of moist earth, (b) a 3-inch layer of sawdust, or (c) sheet metal plates. These top-coverings held in the heat while the goop was burning, forced the heat to penetrate through to the brood layer. Of the three types of covers tested, the pine needle-earth combination was found to be the most practicable.

No further tests with goop have been made; the material is no longer available since war surpluses have been exhausted, and its use requires unusual precautions to avoid spontaneous combustion.

Use of Solar Heat to Kill Broods

Out of the need of substitutes for burning, a method was developed for exposure of infested bark to the rays of the sun. (See "Lethal High Temperatures," Section II, p. 86.) Demonstrations that effective lethal temperatures could be obtained through the use of solar heat opened up possibilities for carrying on control work to advantage during the late spring and summer. The method was given a thorough test on the San Joaquin project (*90*, *U186*). Practical difficulties were encountered, however, in its application. Tedious work was required to get all the bark spread in locations exposed to full sunlight. The method has since been used only when it was necessary to treat trees during the summer period in parks and areas of intensive use where the expense seemed warranted. Keen (*61*) has given a complete description and summary of the method:

> Trees are felled across logs or other objects in order to hold them off the ground. They are then peeled throughout the infested length and the slabs of bark placed in an opening where they will receive the full rays of the sun during the middle of the day. Bark must be very carefully spread, and must not be in the shadow of other slabs or trees. On north slopes or in canyons it must be carried out to an opening or propped against rocks or trees, in order that the sun's rays may strike it at not less than a 45-degree angle. . . . To be successful, however, it is necessary to have summer air temperatures of 85°F. in order that fatal temperatures of 115 to 120°F. may be produced in the bark. Such temperatures do not always prevail during the treating season, especially at high altitudes and on northern exposures, and for this reason the results are erratic.
>
> It can readily be seen that the method is tedious and requires great attention to detail, or it will fail to produce results. . . . In addition this . . . method is more expensive than the peeling or burning methods and is therefore of limited applicability.

Sun curing of bark by turning unpeeled logs so that all of the infested bark surface eventually receives full exposure has been effective with thin-barked trees, such as lodgepole pine infested with the mountain pine beetle (*109*). This modification of the solar heat method was also tested with the western pine beetle, but was found to be impracticable. The thick ponderosa pine bark heats up too slowly when still attached to the log, and many of these logs are so large that turning is a difficult and expensive operation.

Use of Toxic Oils to Kill Broods

In 1932, Norman Gay of the Standard Oil Research Laboratory at Richmond, Calif., offered to cooperate with the Forest Insect Laboratory at Berkeley in the first attempts to develop a bark beetle insecticide. The first experiments were started by Gay (*35*),

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who began by testing a wide assortment of materials. These were mainly mineral oils ranging from heavy viscous grades to the light volatile types; they were sprayed on the infested logs.

It was found that light distillates caused the highest mortality, and that their effect was considerably increased by the addition of soluble insecticides such as naphthalene, creosote, and paradichlorobenzene. An oil-naphthalene mixture, diesel oil of 27 percent API gravity with a saturated solution of crude flake naphthalene gave the best results and was considered to be the most practical formula because of its general efficiency and low cost.

After Gay's preliminary work demonstrated that oil sprays could be used in place of peeling and burning, a long series of tests was conducted by the Forest Insect Laboratory personnel at Berkeley. The practical limitations and possibilities of the method were explored both in the laboratory and on experimental control projects (fig. 61).

Salman (*U263*) tested oil sprays on overwintering western pine beetle broods in the laboratory and obtained mortalities ranging from 22 to 60 percent. Struble (*U298*) tested the oil-naphthalene formula on 39 infested trees and obtained mortalities ranging from 13 to 76 percent. This great variation did not correlate with the amount of oil used or bark thickness. The most important limiting factor, in fact, appeared to be bark texture (*U226*).

In 1934 Struble (*U299*) conducted a series of laboratory tests on bark sections under controlled temperatures and oil dosages. He found no mortality below 50°. From 60° up to 90°, mortality increased with temperature and dosage. A laboratory experiment by Miller (*U198*) showed that at a constant temperature of 60°, mortality increased with the time elapsing after treatment and

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FIGURE 61.—Treating a felled ponderosa pine, infested with the western pine beetle, with a penetrating oil spray.

approached 90 percent after 35 days when heavy dosages of oil had been used.

When the oil spray treatment technique was transferred to control projects in the field, results were erratic. On Sierra National Forest in the fall of 1933, results were so unsatisfactory that the treated trees were burned the following spring (*U300*). This failure was blamed on low temperatures and on thickness and texture of bark on the predominantly large infested trees in this project.

During 1935, Struble and Hensill (*U314*) made a thorough investigation of the toxic and physical properties of oils and mate-

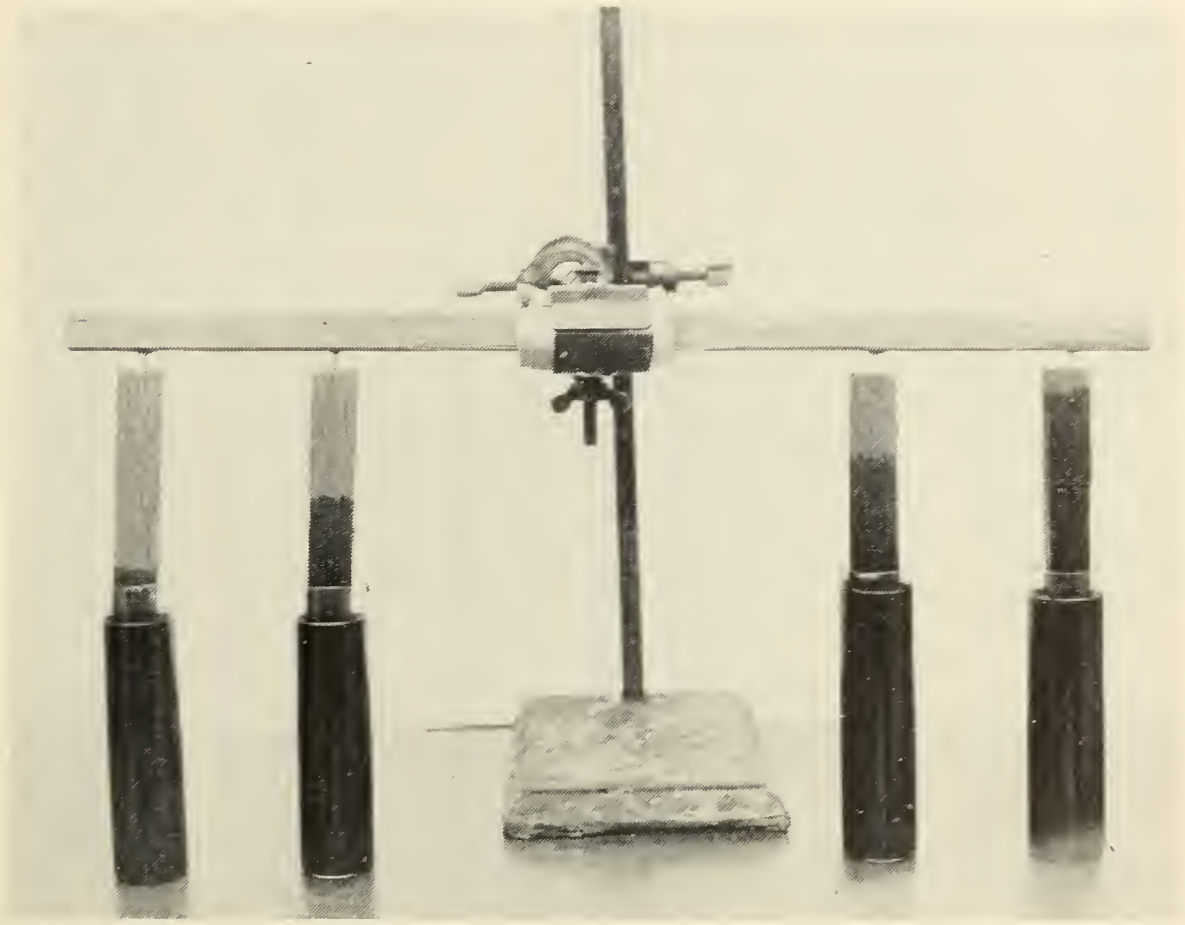

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FIGURE 62.—Apparatus designed and used by George Hensill to determine rate and depth of penetration of toxic oils in ponderosa pine bark of varying texture.

rials used in different formulae, and determined brood mortalities for different conditions. Hensill (*U95*) studied the resistance of western pine beetle larvae to different formulae and the capacity of different oils to penetrate ponderosa pine bark (fig. 62). He summarized results of the experimental work, gave detailed instructions about methods of oil formulae application, and analyzed the costs.

Two oil formulae were recommended: (1) a creosote-diesel oil-lubricating oil mixture; and (2) a diesel oil-naphthalene mixture. Larval mortality resulting from the use of the oil-naphthalene formula was found to depend upon the depth and rate of oil penetration into the outer bark. This varied greatly between individual ponderosa pines, primarily because of differences in bark texture. Higher brood mortality resulted where large larvae, pupae, or new adults were present at time of treatment (*U96*). The oil apparently did not penetrate directly through the bark, but would seep around

bark scales, into ventilating holes, bark crevices, or openings, and reach the larvae through the frass in their larval mines (*U97*).

Results of Hensill's experiments showed that 80 grams per square foot was not adequate, and that extension of time up to 35 days after treatment did not increase mortality of larvae (fig. 63). A dosage of 120 grams per square foot produced complete mortality within 28 days after treatment. It was shown that the penetrating oil control method could be used to advantage only against broods in thin-barked trees, and that it was impossible to obtain satisfactory

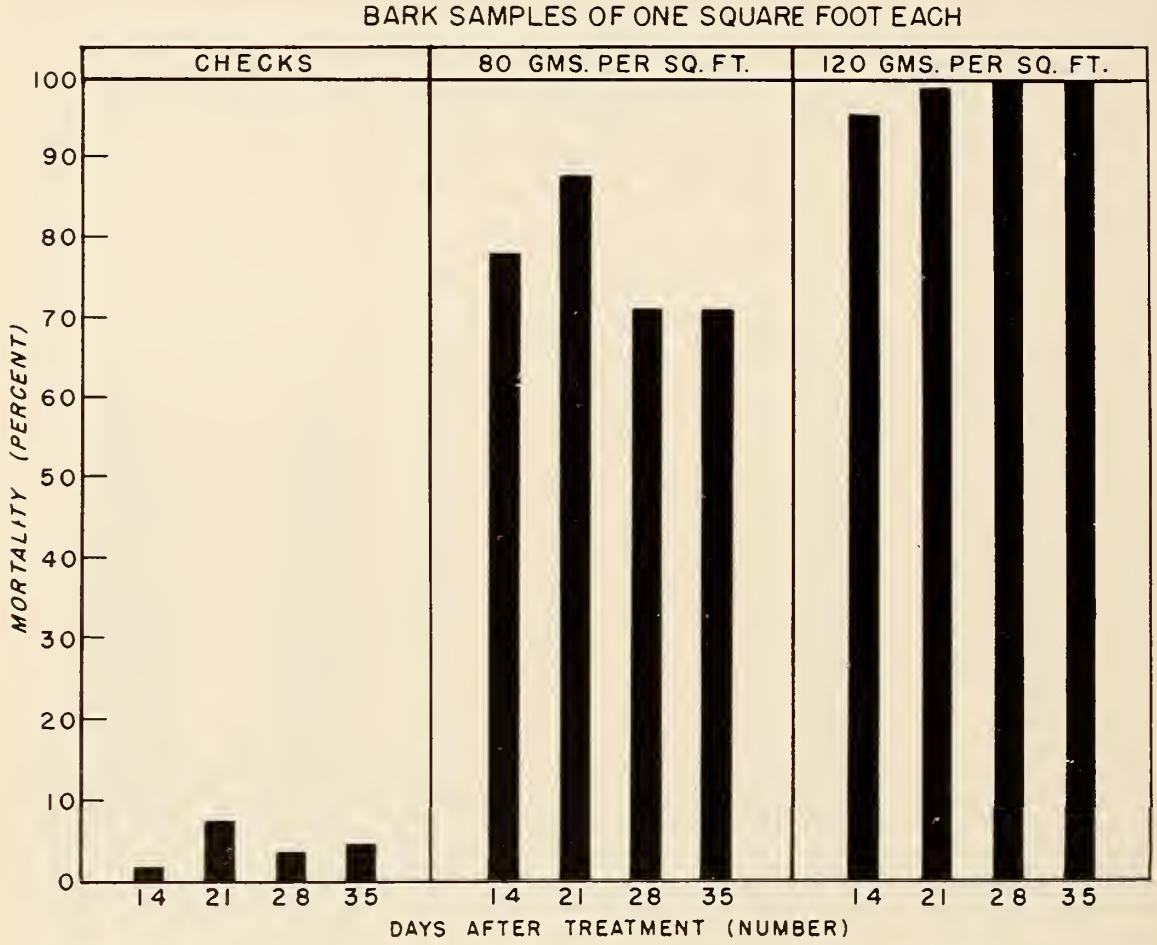

FIGURE 63.—Mortality of western pine beetle larvae in pine bark treated with oil-naphthalene (Formula 21046R) under temperatures ranging from 57° to 61° F.

control on the bottom of logs unless the logs were rolled and the bottom half given a separate treatment.

In 1938 Salman (*119*) summarized the conclusions reached in these experiments with penetrating oil sprays:

> It has been determined that satisfactory mortality of bark beetle broods within or under the bark of infested ponderosa, Jeffrey, sugar and lodgepole pine trees may result from external applications of penetrating oil sprays. The best control has been obtained with a light distillate type of oil in which crude flake naphthalene has been dissolved at the rate of three-quarters of a pound per gallon of oil. Brood resistance, infestation conditions, temperature, moisture, and thickness of bark cause great variation in the brood mortality resulting from the use of the oil spray. In

addition, the difficulties concerned with the transportation of supplies in the forested areas of California and the high cost of the treatment as compared with the peeling-burning treatment limit its use and adaptability.

Experimental results do not yet justify the general replacement of the peeling-burning method of bark beetle control by the oil-spray method. It may, however, be used to supplement other methods during the season of great fire hazard. The use of oil sprays appears to be of value in recreational areas or in commercial timber when infestation conditions or use requirements make it necessary to control forest insects during the summer.

The fact that satisfactory results can be obtained by external applications of contact sprays makes further study of the method desirable. Exact studies of the manner in which environmental factors limit the effectiveness of the sprays should be undertaken. Studies of new materials or combinations of materials, and new methods of application should be made in an effort to increase the effectiveness of the sprays and to reduce the costs of application.

Because of the unfavorable factors that limited the use and effectiveness of penetrating oil sprays, no further attempts were made at spray control of the western pine beetle for many years.

The success shown with thin-barked trees, however, prompted Coeur d'Alene Forest Insect Laboratory to begin investigative work in 1935 to develop penetrating oil sprays for control of the mountain pine beetle in lodgepole pine and western white pine. This work met with great success and developed the use of orthodichlorobenzene in diesel oil as a most effective spray (*U70*). A mixture consisting of one part of orthodichlorobenzene to six parts of diesel oil, the standard spray for this purpose, came into general use for the control of bark beetles in thin-barked trees both in the Rocky Mountain region and the Pacific States.

With the appearance of the newer synthetic organic insecticides during World War II, new tests with toxic oil sprays were started in the hope that some of these new chemicals might prove more effective against bark beetles than those previously tried. Hall made laboratory tests in 1945 with DDT in 5 percent and 10 percent concentrations mixed with kerosene and stove oil (*2*, *U86*). Field tests were also conducted in cooperation with McCloud River Lumber Company. The laboratory trials showed promise, but the field tests were not effective because of thickness of bark and the need to roll the logs to get good penetration on the lower side.

From 1946 through 1949 Patterson continued to test these new synthetic insecticides. The experiments included oil treatment of slash to prevent buildup of engraver beetle populations, protective sprays applied to living trees to prevent attack, and sprays applied to infested bark surfaces of logs and standing trees to kill the broods of emerging beetles. The spray formulae included oil solutions of DDT, BHC, chlordane, toxaphene, and para- and orthodichlorobenzene in varying concentrations.

While the experiments were directed primarily toward engraver beetle control, other pine beetles (*Dendroctonus* spp.) were also

included in a number of tests to broaden the application of results. Patterson (*U231*), in his final report covering the 1949 season, indicated only slight differences in the effectiveness of the different insecticides, but said that the 5 percent DDT-diesel oil formula was the most satisfactory. Although BHC was higher in its initial toxicity, DDT had greater residual killing power and was used in most of the control tests. Patterson's conclusions were:

> Penetrating type sprays were the only kind that gave any promise of success. Results were highly erratic and inconsistent. All the organic insecticides used were highly toxic to bark beetles when in contact with them. Because beetle broods are well protected within and beneath the bark, success in brood destruction is dependent upon the ability of the sprays to penetrate the bark and carry the toxicants to the broods. Penetration of oil diluents is controlled by several conditions, principally by bark texture, density, and amount of surface furrowing. Ponderosa pine offers least resistance to oil penetration, and Jeffrey pine the greatest. There is also wide variation in penetrability of the bark of individual trees of each species, which is not usually obvious from surface examination.
>
> Penetrating oil sprays will consistently destroy broods in ponderosa pine bark up to 2 inches in thickness. Control of *Dendroctonus* beetles was not entirely successful except when the overlying bark was less than 2 inches in thickness. When thicker bark is encountered, the method is not dependable.

In the forests of southern California, where a method of control that would avoid the use of fire was badly needed, experimental work on penetrating oil sprays was continued from 1949 to 1952. The first tests were run during the summer of 1950, using orthodichlorobenzene in diesel oil (1 to 6 by volume) and DDT in diesel oil (5 percent solution). Tests were made both on felled and standing infested trees.

Moore (*U212*), summarizing the results of these tests, stated: "Good results could be obtained with orthodichlorobenzene and DDT penetrating oil sprays providing trees were felled, bucked into logs, and the logs rolled during treatment so that all of the spray could be applied to the logs from above. Orthodichlorobenzene gave slightly better results than DDT; the penetrating oil spray treatment is not as effective against broods in standing trees as against broods in felled trees."

In field tests at Lake Arrowhead during the spring of 1951, Moore found that orthodichlorobenzene gave very good results as a penetrating oil spray "where the average size of the infested trees is under 20 inches in diameter, the bark is thin and dry, and it is not necessary to carry the spray for any great distance."

Also in the spring of 1951, orthodichlorobenzene in oil (1 to 6) was applied to 50 felled ponderosa pines infested with western pine beetle in the Cedar Grove area of Sequoia-Kings National Park. These trees were too large to be rolled, and the results of the test were very unsatisfactory.

About 1950, ethylene dibromide was found effective for control of the Engelmann spruce beetle in Colorado. Further tests at

Coeur d'Alene Laboratory and in southern Idaho indicated that it also had great promise as a toxic spray for control of other bark beetles. L. W. Orr, the first to test ethylene dibromide in fuel oil against the western pine beetle, obtained very satisfactory results in preliminary work in southern Idaho. He stated: "Satisfactory control was obtained when 1½ pounds of technical grade ethylene dibromide were mixed with 5 gallons of No. 1 fuel oil and applied to the bark of ponderosa pine trees infested with the western pine beetle or mountain pine beetle."[7] These preliminary tests were followed by a large-scale application in a control project on Boise National Forest in 1951. Since 1951, this chemical has been used successfully against western pine beetle in southern California and other regions.

After 20 years of searching for a satisfactory toxic penetrating oil spray for control of the western pine beetle, it finally appears that an effective insecticide has been found in ethylene dibromide. However, any use of a penetrating oil spray involves careful supervision and attention to details of formulation and application. And it is still subject to many of the limitations enumerated by Salman (*119*) in 1938.

Residual-Type Sprays

With the development during World War II of new synthetic organic insecticides such as DDT that kill insects on contact with the crystals, the possibilities arose of applying these chemicals as thin deposits on the bark of pines to kill beetles on emergence or to protect trees from attack.

Hall (*U86*) was the first to experiment with a residual deposit of DDT as a protection against attack by the western pine beetle. He found in 1944 that a 2½ percent solution of DDT in kerosene was just as effective as a 5 percent solution in preventing attacks by the beetle on green trap trees and on caged logs where beetles were introduced every 2 or 3 days. The sprayed trap trees also killed other insects, such as the common predator *Temnochila virescens* and ants. Further tests in 1945 using 5 percent and 10 percent DDT in kerosene and stove oil as penetrating sprays applied to infested logs were effective in killing 74 to 98 percent of the brood.

Perry (*U232*) continued these tests with both DDT and benzene hexachloride, and obtained favorable results in treating engraver beetles and the western pine beetle in infested tree sections, and in protecting trees from attack.

Patterson (*U230*) carried on a number of field experiments from 1946 through 1949 testing a 5 percent solution of DDT in stove oil and diesel oil as a residual spray against emerging adults of the western pine beetle. The spray was applied to standing ponderosa pines as a dense mist at the rate of 4 to 6 gallons of spray per tree to a height of about 40 feet. Patterson found that many of the emerging beetles died in their exit holes on coming in contact with the sprayed surface. Others died from contact with the spray on the bark surface. Patterson concluded that "saturation of the outer

[7] In an insert prepared by Orr for U. S. Dept. Agr. Circular S64 (*150*) at the Forest Insect Laboratory, Ogden, Utah, on Jan. 22, 1952.

bark with DDT will result in death of a high percentage of emerging beetles. Diesel oil with 5 percent DDT applied to infested stems in the form of a mist, or atomized stream, resulted in over 90 percent mortality to emerging beetles."

Patterson and Engen (*U165*) conducted a field test with residual DDT spray in April 1949 on standing trees infested wtih engraver beetles and the western pine beetle on the Julian-Cuyamaca control project in San Diego County, Calif. A 3 to 4 percent DDT solution in xylene and diesel oil was applied at the rate of about 3 gallons per tree to a height of 40 feet. This formulation was applied mainly as a bark penetrating spray to kill broods in place, but the residual effect of the DDT deposited on the bark should also be taken into account. The results from caged tests of emergence and attack on green logs were relatively unsatisfactory and erratic.

In 1951, Moore (*U213*) carried out further tests under laboratory conditions with DDT, technical BHC, and lindane. He found that all of these materials were lethal to the western pine beetle after short periods of contact (from 5 to 60 seconds). Infested logs treated with a 6 percent DDT fog showed 96-percent beetle mortality within 48 hours following treatment (compared with a 69-percent mortality after treatment with a 0.5 percent lindane fog and a 36-percent mortality in checks). Moore concluded that control of the western pine beetle and the California five-spined engraver would be possible through the systematic development of formulations and application techniques of residual type sprays.

Miscellaneous Methods of Destroying Bark Beetles

Many proposed methods for killing beetles have gone unrecorded after investigators tested them and found that the results were negative or impractical. Some ideas, however, have been reported upon even though they seem to offer nothing in the way of practical possibilities, and they are listed here in order to complete the record of control experimentation and for such negative value as they may have.

Scoring Felled Trunks

This method, suggested by Hopkins (*44, p. 69*), was apparently based on some experiments made by W. F. Fiske with the southern pine beetle. The method was tried without success in 1912 on the first western pine beetle control project in Klamath Basin (*U42*). A small series of trees containing overwintering larval broods was felled in the fall, and a strip of bark about 4 inches wide was scored for the entire infested length along the top of the trunk. These trees were left over winter and reexamined the following spring.

No exceptional mortality was found in the broods; instead, under favorable moisture conditions the larvae had waxed fat during the winter and appeared to be in better condition than broods that overwintered in standing trees. Development was considerably retarded over that in standing trees. The bark, which had been quite tight when the trees were felled, had loosened by spring so that it peeled without effort. However, the results were so unsatisfactory that the method was never tried again.

Burying Infested Bark in Soil

In 1923 Miller (*U188*) ran a test to see if burying infested bark would suffocate and kill the broods:

> The yellow pine bark sections selected for the test contained about 2 square feet of bark surface. Nine of these sections were collected from the same tree on June 27. The bark at this time contained full grown larvae and first pupae of the western pine beetle. Seven sections were buried in dry soil at depths varying from 2 to 14 inches; as a check, 2 sections were kept under conditions where the brood could develop normally. The new beetles from the check sections had all emerged by August 19.
>
> The 7 sections that had been buried were uncovered on November 15 and were examined to determine the results. It was found that emergence had occurred in all sections and that the beetles had apparently worked their way out through the covering layer of soil. The bark was then shaved up to see if any percent of the brood had died; the mortality found was but little higher than normal, although the broods had been under ground for 142 days. In the sections buried at a depth of 10, 12, and 14 inches, living larvae were still found indicating that their development had been considerably retarded. No dead pupae were found in any of the sections. Low soil temperatures may account for the retarded development of larvae in the sections buried at 10 inches and below.
>
> The conclusion is that the method will not work in dry soil. It may be possible to get better results if the bark is planted in moist soil.

The burying method, never given much consideration, was discarded after this check.

Electrocution

The idea that alternating electrical current could be used to kill bark beetles originated about 1919. Professor W. J. Chamberlin of Oregon State College, at the request of J. F. Kimball of the Klamath-Lake Counties Fire Association, carried out some experiments with high voltage current on infested trees. Chamberlin (*18*) first found that a current of 110 volts was fatal when it passed through the beetles. (The beetles were placed on a wet blotter with the two poles of current very close to the body of the insect.) Then the researcher located infested trees along a transmission line of the California-Oregon Power Company and connected wires so that high voltage of the line could be switched into the trees through contacts at the top and near the bottom. Voltages of 6,600 and 11,000 were applied for periods of about 15 minutes. Chamberlin states that "the beetles were killed for some four feet below the upper terminal, and some were killed near the lower contact." Apparently the effect of the current upon the broods was localized in the bark around the points of contact and was not distributed with enough force through the infested bark to produce any appreciable mortality.

In 1933 the Forest Service and the Portland Gas and Electric Company cooperated in further tests with alternating current. These

experiments, suggested by Clay Allen of the Forest Service, were prompted by the development of a light portable generator for powersaw operation that made it possible to produce high voltage anywhere in the forest. In the laboratory tests, as reported by Keen (*U148*), currents of measured voltages and amperes were passed through sections of bark infested with western pine beetle broods. Several tests were run with varying amounts of volts and amperes, but all results were entirely negative. It was found that the current followed the lines of least resistance—the pitch seams of the bark crevices. As a result, it had no effect in the large bark plates where most of the brood was located. When an attempt was made to kill the beetles in a more conductive medium—wet blotters—the current passed through the blotter but did not affect the insects on the surface.

The results of these tests showed fairly conclusively that alternating current offers no possibility of bark beetle control, regardless of the amperage and voltages used.

Radio Waves

With the development of electronics and the discovery of the lethal effects of high frequency waves upon living organisms, it was inevitable that the idea of trying this method against bark beetles should develop. Tests run by Gordon at the University of California in 1934 and reported by Hensill (*U94*) used plates of approximately 12.5 square inches and a frequency of 250 to 300 mils. Infested bark sections were exposed between these plates for periods of 10 to 15 minutes.

Method of exposure:	*Mortality*
Single bark sections placed flat between plates.	100 percent inside plate areas; 0–8.7 percent outside of plate area.
Two bark sections with wood between placed flat between plates.	7.1 percent inside plate area; 2.6 percent outside plate area.
Bark section placed end to end (longitudinally) between plates.	Zero percent inside and outside plate area.

The only conclusions warranted from these experiments are that radio waves are effective only within the field of the plates, that narrow separation between plates is necessary to obtain mortality, and that because of these limitations radio waves can be of no practical value in killing bark beetle broods with any of the equipment and frequencies now available.

Fumigation

The use of gas to kill beetles has been considered only in connection with summer control work on Yosemite National Park. Experiments were carried out to see if an effective fumigant could be enclosed with unpeeled logs by means of a portable fabric cover in order to eliminate the labor of peeling for solar heat control.

Yuill (*U345*) tried methyl bromide on bark infested by the western pine beetle in 1938. When infested log sections were enclosed in large plyboard containers, 100-percent mortality was obtained with moderate dosages of the gas. However, when a synthetic rubber blanket was used to cover infested logs on the ground, results were

unsatisfactory. Leakage of the gas was so great that mortality was obtained only with very heavy dosages. The difficulties of making a gas-tight fit of the rubber blanket around an infested trunk on rocky or brushy ground were so formidable that attempts to adapt this method to the conditions of actual control work were abandoned.

Injection of Infested Trees

The introduction of toxic chemicals into the sapstream of infested trees to kill broods of the mountain pine beetle has been given a great deal of study in the northern Rocky Mountain Region (*4*). Powdered copper sulfate (mixed at the rate of 8 ounces to 3 quarts of water) was the most effective poison used, although sodium arsenate and zince chloride were also effective. There has been no attempt to kill western pine beetle broods by this method because the egg galleries of this species cut off circulation in the phloem so quickly after attack that a satisfactory distribution of chemicals seems hopeless. Gordon (*U73*) approached the problem by making a laboratory study of the toxicity of certain chemicals that, could be used in ponderosa pine to kill broods by means of injection, but did not carry the tests to trees infested by the western pine beetle.

Stump (*130*) described a method for injection of nicotine sulfate into infested trees by a series of bore-holes with inserted pipes. He claimed that when nicotine sulfate was inserted in this manner near the base of trees, the eggs and larvae of the pine beetle were killed and the parent adults left.

The results claimed for this method were so startling that entomologists at the Forest Insect Laboratory in Berkeley made an investigation of the trees treated by Stump near Mineral, Calif., and conducted some further tests of their own, as reported by West (*U328*). The investigation revealed that the experimental trees described by Stump had been infested by the red turpentine beetle and not by the western pine beetle; also that several of the trees had died since 1936, apparently as a result of red turpentine beetle infestations and chemical injury.

From further tests made by West, it was found that:

> Ten percent nicotine sulfate in sufficient quantities resulted in death of the phloem tissue. Therefore, this compound cannot be recommended for treating living trees. Since there is very little tangential conduction, this method (of injection) would not be effective against insects with any compound unless the trees were practically girdled.

Dr. A. R. Olson of the University of California Chemistry Department advised the Forest Insect Laboratory at Berkeley in 1943 that he had successfully controlled western pine beetle infestations in some trees around his summer home at Dutch Flat, Calif., by injecting 5 to 10 cc. of carbon bisulfide into the cambium layer. This case has not been verified as to species or stage of development of the insect at the time of treatment. According to Dr. Olson, the injection of carbon bisulfide would be valuable as a preventive as well as a control treatment. Tree injection experiments of the Forest Insect Division, on the other hand, have indicated that nonwater soluble compounds such as carbon tetrachloride and carbon bisulfide are not readily taken up in the circulatory system of green trees (*27*).

Injection of High-Risk Trees

Injections of toxic chemicals into living trees to prevent the attack of bark beetles and the introduction of blue-stains and rots have been the subjects of extensive research in ponderosa pine. These methods are forms of indirect control aimed to prevent attacks on susceptible trees until the trees can be reached by logging operations. Even if chemical treatment should kill the trees, investigators said, its use would be warranted if the treatment prevented blue-stains and preserved the merchantable quality of the wood until the trees could be converted into lumber.

West (*U329*) in 1937–38 tested an injection method on Modoc National Forest in California. A series of 50 high-risk merchantable ponderosa pine trees was treated with copper sulfate by the saw-kerf method of injection. During the next 2 years, some of the trees were cut and sectioned to reveal the pattern of chemical distribution in the trees and to determine whether the introduction of insects and fungi had been prevented. The results were entirely disappointing. The chemical was distributed very erratically, especially in those trees with decadent type crowns. In most of the trees, a large amount of the sapwood was not impregnated, and both insects and fungi attacked the untreated wood. Also, after the second year blue-stains developed even in wood where copper sulfate was present. Because of these conditions and the fact that checking became prevalent as the trunks began to season, little merchantable material remained in the treated trees.

Patterson (*U228*) continued this line of experimentation in 1940 seeking better chemicals and ways to overcome their erratic distribution in treated trees. He injected some 205 trees of varying degrees of risk using a wide range of chemicals (fig. 64). The plan called for a period of 5 years on the stump before all of the trees were to be cut and analyzed for the amount of preservation. Final results of these tests were summarized by Patterson (*U229*) as follows:

1. Sapstream conduction of the different chemicals used varied slightly. Sodium arsenite conducted best and copper carbonate least.
2. Conduction through the sapwood of the stem varied within wide limits between individual trees, regardless of chemical injected or risk characteristics. As a class, low-risk trees conducted slightly better than high-risk trees but the difference was not enough to be significant.
3. Conduction in trees appeared to be controlled in large part by age of trees and stem length. In general, young trees of small diameter and low to medium height conducted decidedly better than older, larger trees of greater height.
4. Pitch infiltration in partially transformed sapwood greatly inhibited distribtuion.
5. The inorganic chemicals exhibited highly repellent qualities to bark beetles and wood borers; trees treated with the chlorinated phenols were not resistant to attack by these insects. None of the chemicals fully resisted attack by ambrosia beetles.
6. Blue-stain freely developed in trees treated with all of the chemical compounds used, but it was largely restricted to untreated areas in the sapwood.

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FIGURE 64.—Method of injecting wood preservative into high-risk ponderosa pine. Trees with completed rubber girdles filled with preservative, in process of absorbing chemicals.

7. Stem checking developed in 30 percent of the experimental trees; checking increased in magnitude and extent with prolonged exposure following treatment.

8. Stem rot developed in all of the impregnated trees before the end of the final 5-year period.

9. As a result of these tests, the possibility of holding impregnated east-side California pines without deterioration more than 3 years appears to be remote because of excessive stem checking and rot.

Tree injection has also been applied to prevent insect attack in rustic poles and to keep the bark intact on the logs. Patterson (*U227*) carried out a series of experiments testing methods and materials for this purpose. He produced much better results than those from West's (*U329*) experiments, because of better conduction of the chemicals in younger trees of pole size as compared with mature high-risk trees.

TRAPPING METHODS OF CONTROL

The idea of trapping beetles by means of light, attractive baits, or felled trees has appealed to many workers. Some of the earliest investigators carried out trapping experiments.

Light Traps

Although bark beetles have not been observed to fly at night, one commercial company has attempted to draw them to light traps. In 1931 M. F. Postlewaite, agent for a device known as the Green Cross Trap, installed this apparatus in Stanislaus National Forest near Strawberry, Calif. The main attractive element in the trap was the light of an acetylene burner; it also included a water reservoir covered with an oil for which some attractive properties were claimed. The apparatus was constructed so that insects coming to the light were trapped in the oil and killed. G. R. Struble selected the site for the trap and tended it for six nights during the bark beetle flight period in July. The results of this test were reported in a letter from Struble to Postlewaite:

> It looks rather discouraging for the trap so far as bark borers are concerned. The catches to date have been about the same for each night. The insects caught in order of importance are: (1) mosquitoes (males for the most part), (2) other Diptera including gnats, flies, and some crane flies, (3) miscellaneous moths of medium size, none of which are known to be of economic importance, (4) a few aphis and hymenopterous insects, and (5) a few very tiny Coleoptera (flower beetles). None of the bark beetles were represented in any of the catches. During the day time, no insects have been noted to be in the traps.

Bait Traps

Forest entomologists have also explored the idea of using a chemical to attract western pine beetles to a mechanical trap. The beetle's well-known habit of concentrating in certain trees and avoiding others offered some possibility for the success of this method, because it indicated that the beetles responded readily to some odors or esters peculiar to slow-growing or weakened trees. It seemed that if this odor could be produced synthetically, it might be feasible to attract the beetles to traps in much the same way as the Japanese beetle is trapped by geraniol. This was one of the motivating ideas behind the long series of studies dealing with attraction of the western pine beetle (see Section I, p. 37).

In experiments by Mirov (*U211*) and Person (*U245*), mechanical traps baited with fermenting phloem and used under insectary control did succeed in trapping some beetles. However, none of the chemical substances isolated were as attractive as the natural phloem of slow-growing or weakened trees. Therefore, it was considered improbable that a trap baited with fermented phloem could compete with the attraction of high-risk trees in the forest. An artificially baited trap might fool a few beetles, but even under insectary conditions it failed to fool all of them.

Trap Tree Control

Trap tree control was first defined by Hopkins (*44*):

> The well-known attraction of many species of European bark beetles to weakened, dying, and felled trees suggested to some of the earlier writers on forest insects a method . . . which since that time has been widely recommended and under certain conditions and for certain species of beetles has been practiced. It is the so-called trap-tree method, in which living trees are deadened or felled at the proper time or season to attract the insects and induce them to breed in the bark, where they can be easily destroyed by removing the latter or burning the entire tree.

However, Hopkins does not give the trap-tree method entire approval. He adds that it "may not attract the beetles to the trap trees, but to nearby healthy trees; thus inducing instead of preventing a destructive outbreak."

Hopkins (*44*) considered that the western pine beetle would be very easily attracted to trap logs and would respond to this method of control:

> Under certain conditions, therefore—as in the case of the absence of logging operations and where only a few scattered trees are infested—it may be desirable, as a means of maintaining control, to provide a few trap trees to attract the first generation. This can be done by girdling two or three inferior trees to the heartwood or felling them in June. Then, if they become infested with this beetle, the bark should be removed from the main trunk and burned by the middle of August. Trap trees to attract the second generation should be prepared in August and September and barked before the first of the following May. Usually an average of one to three trees to the acre should be sufficient for this purpose. However, the number will depend largely upon the prevalence of the insect.

These suggestions by Hopkins led to serious considerations of the use of trap trees during the early development of western pine beetle control. According to Miller (*U189*), who summarized the attempts at trap tree control:

> The trap tree differs essentially from the standing infested trees in that when it is attacked the sap flow has been checked and natural resistance in the tree is lowered or entirely lacking. A few beetles can successfully attack and develop broods in a felled tree whereas numbers of beetles must concentrate on a standing green tree with normal resistance in order to overcome the sap flow and make a successful attack. It has been found that the number of attacks per square foot of infested bark surface in windfalls or felled logs varies greatly and is from 50 to 70 percent less than the average for standing infested trees. It was also found that the emergence of new beetles from trap trees is usually about 50 percent less than that in standing infested trees.

At first glance the trap tree method of control seems to offer definite practical advantages, which can be summarized as follows:

1. By careful selection of trees used for traps, beetle populations can be drawn into inferior or unmerchantable trees and thus pre-

vented from attacking valuable trees in the stand. Trap trees can be used both as a method of bark beetle control and as a means of stand improvement.

2. Nature at times provides a considerable amount of trap tree material in the form of windfalls and snowbreak. Such material can often be used to supplement felled trees as a medium for trapping beetles. Then if all trap material is burned or otherwise "treated" at the proper time, beetle populations within an area will be reduced.

3. Traps can be used to localize the infestation within an area to be protected and thus reduce the cost and difficulties of treatment.

Girdled Trees as Traps

Hopkins suggested girdling trees for traps, and at first this was thought to be the best method of attracting the beetles. Chamberlin (*17*) also strongly recommended it. However, the first attempts to use girdled trees were so discouraging that the idea of using this type of trap tree was soon dropped. Miller (*U189*) summarized experiments with girdled trap trees on the Ashland and Northfork studies:

> Girdled trees were found to attract beetles only after considerable interval of time. One tree which was bark girdled in 1916, i.e. the bark peeled to the depth of the sapwood entirely around the base in a band about three feet wide, remained green and up to 1920 had not been attacked. Trees girdled to the heartwood were eventually attacked, but in the case of two trees so girdled at Northfork in April 1920, no attacks occurred until the fall of 1922.

Felled Trees as Traps

Keen (*U127*) kept records on 17 trees felled for traps on the Ashland area in 1916:

> Although the trees were intended to attract *D. brevicomis*, they succeeded in attracting for the most part large broods of *Ips confusus*, *Ips oregoni*, and *Ips emarginatus;* leaving comparatively little area for *D. brevicomis.*

Most of these trees, however, were cut during April and May and were, therefore, exposed to the early emergence of engraver beetles before the western pine beetle was in flight. Keen concluded:

> The trap tree experiment was a failure as far as drawing in broods of *D. brevicomis* from any of the surrounding areas. However, the broods which did attack these trees failed to produce the progeny which is normally produced in standing trees.

Further tests of trap trees were conducted during experimental control work on the San Joaquin project and in Sequoia National Park during the seasons of 1919–21 (*U186*, *U189*). Trap trees were cut at different periods throughout the season to see whether their attractiveness differed with the dates of cutting. It was found that only a small percentage of the trees failed to attract the western pine beetle within 4 to 25 days if the trees were felled between April 15 and September 15. As a rule trees felled after September 15 drew very light attacks or none at all and were not fully infested until the flight period of the following spring.

The Sequoia and San Joaquin projects showed that logs exposed fully to the sun during the summer months were seldom attacked on tops and sides and were generally unsatisfactory as traps. At the same time, logs placed in shaded sites were more completely attacked. This condition, however, was reversed during the late fall and early spring periods; then trap logs exposed to the sun were preferred by the beetles to those in the shade. This discovery led to the practice of using the branches and limbs to cover traps felled during June, July, and August because shading of the trunks increased their attractiveness to the beetles. The trees were limbed after felling, and the branches were draped over the down trunks to form a screen. If the top was insufficient for this purpose, available material such as brush or pine needles was used to make a shade for the entire length of the log.

Composition of Infestation Drawn to Trap Trees

Both the western pine beetle and associated insects are drawn to traps. Keen's first studies (*U127*) showed that the number of pine engravers attracted to traps early in the season may be large enough to occupy most of the bark surface and thus exclude attacks by the western pine beetle. The extensive use of traps on the Antelope and San Joaquin projects has yielded much additional data on the composition of trap tree attack. On the whole, records from hundreds of trap trees have shown that throughout the year the western pine beetle makes up the bulk of the infestation, while the attack of associated insects is highly variable both in incidence and intensity. The followng table summarizes the trap trees attacked by different insect species on the Antelope and San Joaquin projects.

	Trap trees attacked	
Insect species:	*Antelope project (percent)*	*San Joaquin project (percent)*
Dendroctonus brevicomis	100. 0	88. 8
Ips spp. (*oregoni* and *confusus*)	63. 0	32. 0
D. monticolae	12. 5	1. 1
Melanophila (*gentilis*)	11. 0	5. 9
Not attacked by insects	--------	8. 3

The averages shown in the tabulation apply to both mixed and pure infestations. They do not attempt to make a quantitative comparison of the volume of infestation represented by each species and by the mixtures. Records of the various species or combinations of species found in the traps on the San Joaquin project showed a comparison of the percentages of total trap trees attacked according to infestation type, as follows: the western pine beetle, 51.0 percent; engraver beetles, 1.1 percent; the western pine beetle and engraver beetles, 30.6 percent; other mixtures of insects, 8.6 percent; not attacked by bark beetles, 8.7 percent.

These records also show that types of infestation varied greatly according to the season when traps were felled. Engraver beetle attacks were more abundant in the spring and early summer periods, but some occurred sporadically throughout the season.

Traps that were not attacked by bark beetles were found in all tests regardless of whether the trees were cut in June, August, or

September. The number of trees not attacked was higher in the October tests, perhaps because of the fact that most of these late traps were not exposed to attack until the flight period of the following spring. Also the changes that took place in the green phloem of down trees during the winter may have made them unattractive to beetles by that time. However, it seems that there are certain trees that do not attract beetles regardless of when they are cut for traps, and the cause for this has not been determined.

Distance of Attraction to Trap Trees

This question is related to the distances that beetles may fly and also to the potency of the trap log to attract them. In a large infested area, there is no way of telling just where the beetles come from to attack a trap or how far they may have traveled (see "Distance of flight," Section I, p. 50). Records show that in a few cases beetles have been attracted to trap trees placed outside of the pine type for distances of 1 to 2 miles. These records indicate that the attraction to a trap tree is a strong one, but they shed very little light upon flight distances to traps within the pine type where susceptible green trees compete with the traps as centers of attraction.

Use of Trap Trees to Supplement Direct Control

The first attempt to use trap trees on a large scale was begun in 1921 by the Long-Bell Lumber Company in northern California on 52,000 acres of eastside pine type in a control program known as the Antelope Project. Reports by Patterson (*U219*) show comparative volume of standing trees, trap trees, and windfalls treated on the Antelope project, 1921–23.

Year:	*Standing trees treated*		*Trap trees treated*		*Windfalls treated*	
	(*no.*)	(*bd. ft.*)	(*no.*)	(*bd. ft.*)	(*no.*)	(*bd. ft.*)
1921	3, 530	2, 594, 550	660	551, 610	163	204, 740
1922	1, 623	1, 444, 830	376	359, 060	----	----------
1923	93	76, 760	80	48, 190	----	----------
Total	5, 246	4, 116, 140	1, 116	958, 860	163	204, 740

The strategy in this project called for control by fell-peel-burn of the overwintering infestations and maintenance work using trap trees during the summer. Trap trees, it was believed, could be treated more cheaply and effectively with less fire hazard than standing infested trees, which were scattered and difficult to find. The traps were felled at convenient locations, covered when necessary, and treated either by burning or sun curing. In 1921, two series of traps were felled, one in June and the other in September. In June of 1922, another series of trap trees was felled. The number of trap trees in each series was based on an estimate of the recurring infestation following previous control work. Traps were provided to absorb approximately 12 percent of the expected infestation.

All trap trees were more or less heavily attacked soon after they were placed. Records in the first annual report show that the western pine beetle attacked 100 percent of the trap trees. However, engraver beetles (two species) were also present in 63 percent of the traps, the mountain pine beetle in 12.5 percent, and the pine flat-

headed borer in 11 percent. In trees felled in June, the broods developed rapidly and were treated during the later part of July and early August. These trees peeled easily and were treated with a minimum of labor and time. Treatment of the trees felled in September was not as successful; the broods developed slowly, overwintered in the trees, and were treated with difficulty the next spring. Since the infestation was greatly reduced by the third year, only a few traps were prepared, and control work was discontinued after the trees were treated. Because of rapid logging of the area, further maintenance work was unnecessary.

Patterson's (*U219*) conclusions regarding trap trees on this project were:

> As a successful form of control the method is somewhat doubtful in efficiency. The trees were fairly heavily attacked and no doubt drew and localized a large amount of infestation. However, there was a tendency to create group infestations in standing trees adjacent to traps. This was the noticeable effect of the method on this project; a number of instances were noted where these groups amounted to 4 or 5 standing trees per group.

Influence of Trap Trees on Surrounding Infestation

Trap trees were used on the San Joaquin project in 1920 and 1921 to supplement the fell-peel-burn method of control. During each summer, enough trap trees were placed at selected widely scattered but accessible points to absorb the part of the infestation that was estimated as missed in spring control work on the overwintering population. During the second season of the project, the volume of infestation in standing trees increased in spite of the available trap material.

An attempt was made during the 1922 season to determine how much of the seasonal infestation could be drawn into traps. The experiments were in two phases: (1) An area in which all infested trees had been treated was surrounded with a ring of trap trees to determine whether the beetles would cross over the trap ring in order to attack standing trees within the cleaned area; and (2) a line of trap trees was extended across an infested area to determine effect in absorbing beetles within a mile zone on either side of the trap line.

For the first phase, a circular area one-half mile in diameter was selected in the pine type of Chiquito basin. During the spring, this circular area was cruised several times; all infested trees that could be located were treated by the fell-peel-burn method. On June 7 a ring of trap trees spaced 4 chains apart was placed around the perimeter of the circle to absorb the attack of the first seasonal generation. A second ring of trap trees was placed August 7 for the second seasonal generation, and a third series on October 7 for the partial third generation. All trap trees were treated by burning as soon as they became fully infested.

Throughout the season, the area within the circle was kept under close watch, and infested trees were treated as soon as they were detected. Under these conditions it was assumed that (1) any trees attacked within the circular area during the course of the season would be attacked by beetles that came in from outside of the circle,

and (2) in order to reach these trees the beetles would have to cross the line of trap trees. Such behavior, it was assumed, could be explained only by the fact that certain standing green trees within the circle were more attractive to the beetles than the trap tree material. Results at the end of the season indicated that seven large ponderosa pines were attacked within the circle, some of them located very close to its center.

The second phase of this study was also located in the pine type of Chiquito basin. The traps were placed 10 chains apart in a nearly straight line about 6 miles long. The first series of traps was felled June 14, the second series August 18, and the third series October 10. The traps were treated as soon as they became fully infested so that no new broods of beetles would escape from them. The mile zone areas on either side of the trap line were examined at intervals during the season, and the locations of newly attacked trees were plotted to determine their distance from the nearest trap tree. At the end of the 1922 season, the infestation records were summarized for the year that the traps were in effect, and also for the preceding year:

		Standing trees attacked	
Year:	*Trap trees placed*	*0–½ mile zone*	*½–1 mile zone*
1921	0	69 (96,870 bd. ft.)	96 (48,200 bd. ft.).
1922	91 (16,000 bd. ft.)	101 (132,750 bd. ft.)	33 (60,080 bd. ft.).

The board-foot volume of the 1922 infestation increased over that of the preceding year by 37 percent in the 0 to ½ mile zone and by 25 percent in the ½ to 1 mile zone.

These results appear to show only that the traps did not draw beetles away from stading trees to any greater extent in the vicinity of the trap line than they did from a distance of ½ to 1 mile. Actually, the increase of infestation in standing trees was greatest in the zone nearest to the trap line. This trend is further emphasized by the fact that several groups of 4 to 14 trees were attacked in the vicinity of the trap line, thus indicating that beetles were drawn to the general locality of the trap line where they attacked both standing trees and traps.

Summary of Trap Tree Control

Out of the various trap tree studies and the attempts to use traps as a control method, the following points have been established (*U189*):

1. The western pine beetle is attracted to nearly all ponderosa pines soon after they have been felled. Certain trees, however, will not attract this beetle even though they have been carefully prepared as traps.
2. Girdled trees do not make satisfactory traps.
3. The attractiveness of trap trees depends upon fairly exact moisture and temperature conditions in the phloem. During the months of June, July, and August it is necessary to shade the upper sides of fallen logs in order to induce attacks. In the spring and late fall, beetles are not attracted to traps in cold shaded sites.
4. Western pine beetles, in trap logs produce less progeny than in standing trees (*U127*).

5. Associated insects, such as several species of pine engravers, the mountain pine beetle, and flatheads, are attracted to traps and enter into various combinations of infestation types with the western pine beetle. On general averages throughout the season, however, the western pine beetle constitutes 75 percent or more of the volume of infestation drawn to trap trees.

6. Experiments have shown that even if trap material is readily available to the beetles in flight it will not keep the beetles from attacking attractive standing green trees. Beetles will bypass traps to attack standing trees, and groups of standing trees will sometimes be attacked in the vicinity of trap trees. Thus trap trees appear to have no effect in drawing beetles away from standing trees or in lessening the number of standing trees attacked.

7. Increasing the volume of trap trees will not prevent an increase of infestation when conditions favor this trend, either in the immediate vicinity of the traps or in zones up to one mile distant.

8. The cutting of green trees for traps is of doubtful value because the control effects are too slight to warrant the waste of timber resulting from this method.

9. Where creation of trap-type material is unavoidable, as in the case of windfalls and right-of-way clearings, the preparation of this material for traps and subsequent control treatment may be warranted as a control measure. No sacrifice of material is involved in such a case and the practice can be used to destroy some of the beetle population in the area.

Economic problems, not fully covered in this summary, can add many difficulties to the trap tree method: Hopkins' (*44*) suggestion of providing an average of 1 to 3 trap trees per acre would amount to from 640 to 2,000 trap trees per section. Typical epidemics affect only some 50 to 500 per section. The added cost of treating these extra infested trees would be prodigious, and would materially increase the total of direct control costs. Moreover, trap trees must be treated on schedule, before broods emerge; otherwise felling trap trees simply makes a bad situation worse.

CONTROL EFFECTS OF LOGGING OPERATIONS

Entomologists have long suspected that the trapping effect of green logs on large-scale logging operations had considerable effect upon surrounding beetle populations. At one operation in Idaho, logs were intentionally left in the woods long enough to serve as traps. Beal (*U5*) quotes a report by Keen saying that "on the southern Oregon-northern California project, two of the cleanest areas (containing the fewest infested trees) were adjacent to regions where continuous logging had been in progress for several years; and in one unit, a reduction of 60 percent in infestation—equal to the best results obtained by artificial control work—followed the beginning of logging operations on adjacent ground." These and other observations in the pine lumbering areas indicated that regular logging operations do have some effect in reducing beetle populations. However, it was not until detailed studies were undertaken that some appraisal could be made of the extent to which green logs may absorb attacks and carry beetle populations out of the forest.

Studies in Southern Oregon, 1930–32

Beal (*U5*) started a comprehensive study in 1930 near Klamath Falls, Oreg., to determine the effect of logging operations on beetle population. This study was on a large logging operation in a unit where a western pine beetle infestation was increasing. With the daily output of logs about 300,000 board feet or 40 carloads, sufficient green trap material was available to absorb very large beetle populations.

Beal used a standard method of log examination designed to show the amount of bark area that had been attacked by the time the logs were removed from the forest. His examinations included 696 trees selected as samples of the total amount of green trap material. In addition, periodic examinations were made to determine the trend of the infestation in standing trees on the operation and adjacent territory. Results were summed up by Beal (*U8*) in his final report:

> Attacks on felled trees vary throughout the season and appear to be influenced chiefly by the number of beetles in flight and the quantity of material available. In an operation removing daily 300,000 board-feet of logs 51 percent contained beetle attacks after an average exposure of about two weeks.
>
> The frequency of the attack varied with the exposure from 4.4 percent of total bark examined on the top side of logs to 20 or 30 percent on the sides and 36 percent on the bottoms. The attack varied with the season from 0 in April and October to nearly 50 percent in August, the peak of the flight period.
>
> Beetles concentrate chiefly upon the middle and basal portions of felled trees, but in practically all cases keep out of the top sides of the logs. Beetles are sometimes attracted to logs less than 4 days old, but most rapid absorption of beetles occurred on logs from 4 to 10 days old.
>
> The beetles appeared to concentrate their attacks on definite log groups rather than spread out evenly over all logs on the ground. These favored logs continued to absorb beetles until they were removed from the woods.
>
> The attractive influence of felled logs is relatively local. Beetles do not appear to be attracted to this material over distances greater than about one-half to three-fourths of a mile.
>
> It does not appear necessary or especially advantageous to leave logs in the woods longer than about 2 or 3 weeks for the purpose of absorbing beetle attacks. During heavy flight periods and in the middle of summer when danger from bluestain is greatest, they may be removed from 10 days to 2 weeks after felling with considerable assurance of removing a great many beetles with them.

As a measure of the effect of the operation upon the trend of infestation within the general unit, the study failed to give conclusive results. The volume of standing infested trees within the unit was relatively high, averaging 177 board feet per acre, and continued to increase during the progress of the logging operation. Beal stated:

> Logging had no apparent effect upon the Clover Station unit as a whole, because on it during 1929 and 1930 the infestation increased irrespective of logging or the trend of infestation through-

out the region. This has been increasing at a uniform rate since 1926, 3 years before the beginning of logging operations. It is self-evident that the logging of one-fifth of the entire unit, since it was in a heavily infested portion, materially reduced the total volume lost. However, the losses outside the logged area increased. It will be necessary to continue the surveys over a period of years before the influence of logging can be more accurately determined.

Beal also gave some attention to logs on right-of-way clearings, which usually were in better shaded positions than those on the main logging area. He found that "right-of-way logs appear to be very attractive to the western pine beetle and to *Ips*, especially *Ips confusus*."

Studies at Blacks Mountain Experimental Forest, 1941

Johnson (*U116*) made examinations in 1941 on the sanitation-salvage logging operation at Blacks Mountain Experimental Forest. This study was undertaken because it was believed that the light sanitation-salvage cut at Blacks Mountain provided conditions that differed in the amount and nature of trap material from heavy cuttings like those on the Weyerhaeuser operation studied by Beal (p. 302). Instead of a concentration of logs representing practically all of the commercial stand, sanitation-salvage logs were from selected risk trees considered to be susceptible and composing less than 25 percent of the stand. For the most part these risk trees were widely spaced throughout the green stand. Since some low-risk trees were cut for silvicultural reasons, the Blacks Mountain operation afforded a favorable opportunity to determine whether logs from high-risk trees were more attractive to beetles than those from low-risk trees.

Johnson's methods of sampling and recording were similar to those used by Beal (p. 302), although the volume of material studied was considerably less. Some 128 ponderosa pines and 3 Jeffrey pines, amounting to a 9-percent sample of all logs removed on the operation, were analyzed. The 1941 infestation on the Blacks Mountain area was very light, averaging under 50 board feet per acre; also, the seasonal period of attack and flight was relatively short for that season. These conditions may have had much to do with the lack of pertinent results obtained from this study. Johnson found that:

> Sixty-six percent of the ponderosa pine logs sampled gave no evidence of attack. Infestations were uneven and one-sided in the logs. The trapping of considerable numbers of beetles in logs seems to depend upon the fortunate coincidence of a number of distinct factors. It could not be shown that sufficient trapping actually occurred in 1941 on most areas treated by sanitation-salvage to markedly affect the beetle population in these areas. The risk ratings given to trees previous to cutting had no apparent relation to their attractiveness to beetles. In a sample limited to 55 trees, the percentage of attack in each risk class was: Risk 1, 23.5 percent; Risk 2, 25.0 percent; Risk 3, 33.3 percent; Risk 4, 12.5 percent.

Johnson considered the sample too small for reliable conclusions.

CONTROL THROUGH LOGGING INFESTED TREES

Removal of infested trees from the forest for utilization can be considered a method of reducing beetle populations, provided the logging operation is timed so that broods can be destroyed or transported to some distant point where emerging adults cannot find living trees to attack. Hopkins (*44*) suggested three optional methods for the disposal of infested bark: (1) transporting the infested trunks a sufficient distance (20 to 50 miles away) from any living spruce or pine, (2) placing the logs in water, and (3) converting the logs into lumber and burning the slabs. A number of logging control operations in the western pine region have employed these methods.

Transporting the Infested Logs

Evenden (*33*) described the first project to control a western pine beetle infestation by transporting the infested logs. The operation was located on a tract of about 3,000 acres in southern Idaho. Finding that from 15 to 17 percent of the ponderosa pine timber had been killed in a few years by the western pine beetle, working plans were moved ahead about 10 years and timber cutting started in August 1922. Both green and recently killed trees were felled and removed to the mill some 30 miles away. The green logs were left in the woods for not more than 4 weeks to absorb attacking beetles. In this way, the bulk of the infestation was removed from the woods. The project closed in the fall of 1923, and in August 1924 an examination of timber surrounding the cutting failed to show any infested trees within a half mile radius.

Since the advent of truck logging during the 1920's, many projects for control of the western pine beetle have been carried out by trucking infested logs over long distances to mills. Usually these projects have included the salvage of merchantable snags as well as the removal of currently infested trees. From an insect control standpoint, they have not been too successful because of failure to remove all of the infested logs from the entire unit before beetles emerged in the spring (*U103*). Except for the case reported above, no studies seem to have been made to determine just what minimum distance of removal is required to prevent reinfestation of a control area.

Submerging the Infested Logs

The submerging method, which Hopkins (*44*) describes as "placing the logs in water," has seldom been applied on direct control projects. There have been cases, however, where infested trees found on logging operations have been put in the millpond before sawings, because the operators assumed that this would destroy the broods. The first attempt to use this as a method for direct control gave some unexpected results, as described by Keen (*61, p. 26*):

> . . . In the summer of 1922, . . . Mr. J. M. Miller and Mr. R. D. Hartman, placed a quantity of *Ips*-infested poles, which had been cut in the construction of roads, in the lake, to prevent these

beetles from escaping and attacking green timber. The poles were later removed and cut into stovewood. The surprising thing encountered in this work was the fact that the beetles were not killed by a submergence of several days or even several weeks.

Following this experience, Mr. Wagner, under the direction of Mr. Miller, carried on some experiments at Northfork, California, with the submerging of yellow pine bark infested with the western pine beetle. Sections of bark were submerged in a spring, in water of a constant temperature of 70°F., and a section was removed and examined each week. Two and 3 weeks' submergence failed to kill any high percentage of the broods, and 5 weeks' submergence was required to bring about 100 percent mortality. As yet no tests have been carried out to determine the efficiency of the method in killing bark beetles in logs placed in mill ponds. It is quite possible that many logs would always float with one side exposed to the air, and that some of the beetles would escape from this portion of the log. It might also require more than 5 weeks to kill those broods which were submerged.

Converting Logs Into Lumber and Burning the Slabs

Logging of infested trees is a common method of control. On a number of projects, this operation has also included log hauling for a considerable distance and log storage for a time in a millpond. Keen (*66*) describes a typical operation in which logs were milled in the woods:

> In the fall of 1928 the Pickering Lumber Co., having contracted to carry on beetle control on a unit of 15,000 acres in Modoc county, Calif., comprising both the company's and national forest lands, decided to salvage this timber and burn the infested bark at the mill. A small mill was constructed near the center of the area. The infested trees were located by a survey crew in the usual manner. The trees were felled and then, with tractors and fair lead arches equipped with crawler wheels, these trees in full tree lengths were hauled to the mill. The average distance of haul was about 2 miles, but some of the trees were brought in from a distance of 5 miles. About 2,000,000 board feet were salvaged in this manner.
>
> The costs of this operation compared very favorably with the cost of the old burning method and the treatment was every bit as satisfactory from the standpoint of disposing of the bark beetles. Where the old method would have involved a direct outlay of $4.50 per M b.m. of timber treated, with no return from salvage, the method used cost $6.58 per M b.m. to bring the trees to the mill, with an estimated value at the mill of $8 per M b.m., or a net profit on the operation of $1.42 per M b.m.

After describing two other operations by private timber companies in northern California and Oregon to control beetles by logging, Keen analyzed the economics of the method and concluded that "the salvage method of beetle control can be carried on to good advantage and at a considerable saving over the old methods of control."

Values Salvaged From Beetle-Killed and Abandoned Trees

The great advantage of control through logging of infested trees is the utilization of the material. The value of the salvaged trees helps to defray all or part of the cost of the control operations, the proportion depending upon lumber values that can be realized from the logs.

Boyce (*7*) made the first study of the progress of blue-stains and rots in beetle-killed trees (see "The Role of Micro-Organisms," Section III, p. 142). He appraised the amount of blue-stain and decay in beetle-killed trees that were cut and left in the forest, and he concluded that by the end of the second season after attack, the volume of merchantable wood in abandoned trees is so small that it is of little commercial importance.

Patterson (*108*) describes a salvage-control operation in Jackson County, Oreg., during the spring of 1928. Infested trees were logged and milled along with any abandoned trees that contained enough merchantable material for salvage. Patterson determined the percent of cull in a series of these salvaged trees. Excluding blue-stained wood from the cull status because this material, although degraded, could be sawed into boards and sold, he found that:

> Beetle-killed trees do not deteriorate greatly during the first two seasons (after attack), but after the second season they decay with extreme rapidity, so that by the fourth or fifth season the sapwood is a total loss commercially and the heartwood is badly checked and worm eaten.

Jaenicke (*U103*) reported a salvage operation at La Pine, Oreg., carried out between June 1 and November 1, 1930, in which 1,200,000 board feet of infested and abandoned ponderosa pines were salvaged from 10,000 acres. The blue-stain deduction amounted to 20 percent of the gross scale of trees over 22 inches d.b.h. About one-third of the trees were infested, the others abandoned. In another salvage-control operation on the China Hat sale area in the spring of 1936, 1,127,000 board feet of infested ponderosa pines were cut and logged from 4,120 acres (*U106*). More than 90 percent of the sapwood of these trees was blue-stained, representing 50 percent of the total volume scaled. The effect on beetle control was not reported.

In 1934 and 1935 logging of infested and recently abandoned trees was used instead of direct control on two large-scale salvage operations by private lumber companies in northern California. These operations were stimulated by epidemic infestations causing the accumulation of an immense amount of dead pine in the vicinity of current logging operations (*U280*). On the Susanville operation, a complete mill-scale study was made by the California (now the Pacific Southwest) Forest and Range Experiment Station to determine the lumber grades yielded by the salvaged trees. Both projects were reported upon by Salman and Johnson (*U285*), and Johnson later published (*55*) on the results of both the salvage and control phases, summarizing as follows:

> Nearly 5,000,000 board-feet of dead and dying yellow pines were removed from the woods and utilized in nearby sawmills. Ento-

mologists cooperating in the study were interested in determining (1) the relationship between bark beetle development and blue-staining and (2) the control effect of the salvage operations.

Infestation patterns made from bole examination of felled infested trees were used in demonstrating a significant correlation between the blue staining and the insect species present and between the staining and brood development. Degrade from blue staining amounted to as high as 50 percent in trees containing advanced broods of *Dendroctonus*, *Ips*, and *Melanophila*.

A decline of 40 percent in infestation the year following salvage was noted. Infestations in check areas for the same period remained unchanged or slightly increased. The reduction in loss obtained on the salvage area was approximately the same as that following a direct control project accomplished under very similar conditions on a nearby area.

The rapid development of blue-stains in the sapwood soon after a tree is attacked has been the major factor discouraging the logging of infested trees as a control measure. (For discussion of "The Blue-Stain Fungi," see Section III, p. 142.) The amount of degrade found in lumber produced from infested or abandoned trees is usually so great that the product cannot compete favorably with material from sound green trees, even though the blue-stained boards are sound and adaptable to many uses. For interior finish, however, stained boards may have certain decorative advantages. In one case, the McCloud Lumber Company found a temporary market for blue-stained ponderosa pine salvaged from beetle-killed trees which brought prices equal to the best grades of unstained lumber. If other special uses for blue-stained lumber were developed, the higher values that would be realized from salvaged beetle-killed trees would make such control operations highly profitable.

In the mill-scale study described by Johnson (*55*), the species of infesting insect and the stage of brood development were determined before the logs were put on the saw. The correlation of these data with the amount of blue-stain deduction shows the rapidity with which the fungus develops in sapwood:

Brood Stage:	*Blue-stain deduction (percent)*
Parent adults, eggs, and small larvae	10
Small and large larvae	25
Large larvae, pupae, and new adults	50

In 1941 Whiteside (*U332*) made a study of all the salvage logging projects from which data were available, and he summarized what was known about the merchantability of salvaged beetle-killed lumber. In general, it was shown that if trees are salvaged during the season of attack, most of the lumber is still sound but may be degraded as much as 50 percent because of blue-stain; the second year after attack, rots have set in and from 40 to 60 percent of the material must be culled; and for the third year after attack, the cull amounts to about 75 percent. In the third year, only the heartwood core of the log is still sound.

FACTORS INVOLVED IN CONTROL PLANNING AND STRATEGY

The decisions required in recommending, planning, and executing bark beetle control projects are concerned with questions of economic benefits, forest policy, and control strategy as well as technical knowledge of the beetle and of control methods. Control planning involves such questions as: How large an area should be included in the control unit to insure protection from outside infestation? How intensively should the area be covered by control work? Under what conditions is control warranted? The answers to many such questions must be found in deductions drawn from experience with control operations rather than from biological studies. However, a number of studies have been made of certain problems that affect control planning and policies, and these will be reviewed here.

Methods of direct control are designed to accomplish control by rapid reduction of beetle populations. Although the methods themselves are fairly elementary and simple, their success usually depends upon an understanding of the principles involved; on knowing when, where, and under what conditions control should be undertaken. Control projects require careful planning for the best results (*110*).

Hopkins (*44*) discussed these problems of strategy, and was the first to lay down the principle that attempts to exterminate the beetle are unnecessary:

> It must be kept in mind that the beetles must occur in great numbers in order to be successful in their attack on healthy trees. If their number is reduced and kept below that required for killing trees they can do no harm. Therefore in the case of a destructive outbreak it is necessary to destroy only from 50 to 75 percent of the beetles in order to bring them under complete control.

This original policy statement of Hopkins became known as the "percentage principle" of control and aroused a controversy, which is discussed later. Under the topics of "Requisites for successful control," "How to check and control an extensive invasion," "How to control a limited attack," and "How to maintain control," Hopkins (*44*) discussed further the general principles underlying direct control policy. However, his statements apply to beetles of the genus *Dendroctonus* as a group rather than specifically to any one species. It should also be kept in mind that no western pine beetle control projects had been undertaken. Hopkins' ideas of control strategy must necessarily have been based on his knowledge of the habits and behavior of the beetles and not on experience with actual control.

Some of the questions of basic control policy and procedures appear to be of far greater importance than others, but all must be taken into account if control work is to be undertaken on a sound basis.

Boundaries of the Control Area

Essential to intelligent planning for control is the determination of a control area. The selection of boundaries may be regulated by a number of considerations, the most important being the extent and distribution of the epidemic infestation. However, quite often

a large area of infestation can be broken down into smaller units to be worked independently. These may be blocked according to cooperating ownership, topography, and type barriers. Usually the boundaries are determined by the combination of a number of factors. The paramount purpose, of course, is to select an area where the results of the first season of control work will not be upset by an influx of beetles coming in from outside areas.

The ideal control area is an infestation unit, such as that described in Section IV, p. 271. In general practice, control areas usually have conformed to one of the following types:

(1) Small, localized infestation centers that contain the only serious infestation within a much larger forest area.

(2) Areas containing a widely distributed infestation, but well isolated from other bodies of infested timber by topographic barriers, breaks in type, or both.

(3) Areas that have no satisfactory boundaries of topography, type barriers, or breaks in the distribution of infestation, but which are considered to be so large in extent that control results will not be quantitatively affected by beetles infiltrating from adjacent areas.

The problems of selecting satisfactory boundaries for control units are most frequently encountered under the third type of area. For this reason, considerable study has been given to the flight habits of beetles, and to the character of the reinfestation developing along the edges of control areas that are exposed to adjacent infested timber stands.

In 1925 Keen (*U138*) made an analysis of data from the southern Oregon-northern California control project to determine the extent to which the infestation within the controlled area had been affected by adjacent untreated stands. Most of these data came from the Owens unit where no satisfactory natural boundaries could be found. The control work had been extended up to section lines in continuous pine type leaving adjacent similar sections untreated. Keen found that:

> Only on the edge of the area and within the first mile did the infestation show an increase when adjacent to untreated sections. This would suggest that after two periods of flight the adjacent infestation had only drifted back into the area for one mile.

Similar records on this zone of control influence were obtained by Patterson (*U222*) in 1925 in control work then in progress on and adjacent to Klamath Indian Reservation. His control area consisted of a block of 26,000 acres, which was a part of a much larger area of infestation. Natural control boundaries were found for three sides of the tract, but the remaining side consisted of a township line with heavy infestation in pine type outside the boundary. The tract was treated with fell-peel-burn control during the spring period and followed this with summer maintenance work, particularly along the boundaries adjacent to infested timber. In summarizing the results, Patterson reported:

> It was fully expected that the beetles from the untreated outside area would reinfest the treated stands along the exposed border. This occurred to some extent during the flight periods which followed the spring control work, although the amount of this

reinfestation was far less than expected. The invasion was limited to a strip of forest one-half mile wide which lay along the border. An attempt was made to combat this during the summer and fall work by treating the trees attacked as soon as they were discovered. Many of the trees in the fall work were located along this strip and their treatment undoubtedly prevented further spread into the area. An interesting feature of the encroachment of the infestation along this border into the controlled area was the rate of its advance which was gradual and progressive. It did not advance further than one-half mile during the season.

On the San Joaquin project, 1920–24, special efforts were made to determine the width of the zone within which an infestation on a treated area is affected by beetles from an adjacent untreated area. In summarizing the results of this project, Miller (*U190*) reported that on the Forked Meadow unit, which was worked intensively in an attempt to exterminate the beetles, "practically all infested trees that developed in this unit during the 1924 season could be accounted for by beetles coming from infested trees not over one mile distant." This extermination unit was exposed on one side to an untreated area without a natural barrier.

These records and other observations have all served to support the idea that a buffer zone of about one mile is necessary for the protection of a control area where natural boundaries are lacking. It is obvious that an area of four sections, 2 miles square and surrounded by an untreated area, is too small for a control unit because any part of the area would be within 1 mile of the boundary. However, a square area of 16 sections would have 4 sections or 25 percent of the control area in the center protected by a buffer zone one mile wide; or a township with 36 sections would have 16 sections or about 45 percent of the control area so protected. Circular areas would, of course, increase the percentage of protected areas in proportion to the one mile zone around the perimeter. Where no natural boundaries are available, it would be necessary to select larger areas of several townships in order to have a control unit that would not be subject to serious reinfestation from surrounding untreated areas.

In actual practice, the boundaries of control units have usually been determined by a combination of factors, and the areas have shown extreme variation in size. From an administrative viewpoint, the optimum size of a control unit is one that can be covered in one control season by about 25 men. On the average, this has involved from 10,000 to 20,000 acres of pine type. Most desirable of all is a unit of about this size which consists of a natural basin or watershed where the work can be started early at lower elevations and carried into higher elevations as the season advances.

Selection of Control Methods

Decision as to the method of direct control to be used must be governed by the conditions of the area, available labor, and equipment, and the seasonal timing of the control operation. Under high fire hazards, the fell-peel-burn method must be modified to meet

safety requirements, or solar heat, oil treatment, or other methods must be substituted. From a practical standpoint, the selection of the method to be used must be left to the judgment of those responsible for the planning and supervision of a project. There have been no special studies that will serve as a guide to these important decisions.

Seasonal Timing of Control Work

The seasonal period when control can best be conducted is dependent upon the factors of latitude, elevation, and climatic variations influencing flight periods and dormant periods of the beetles. Such factors also affect the accessibility and working conditions in control

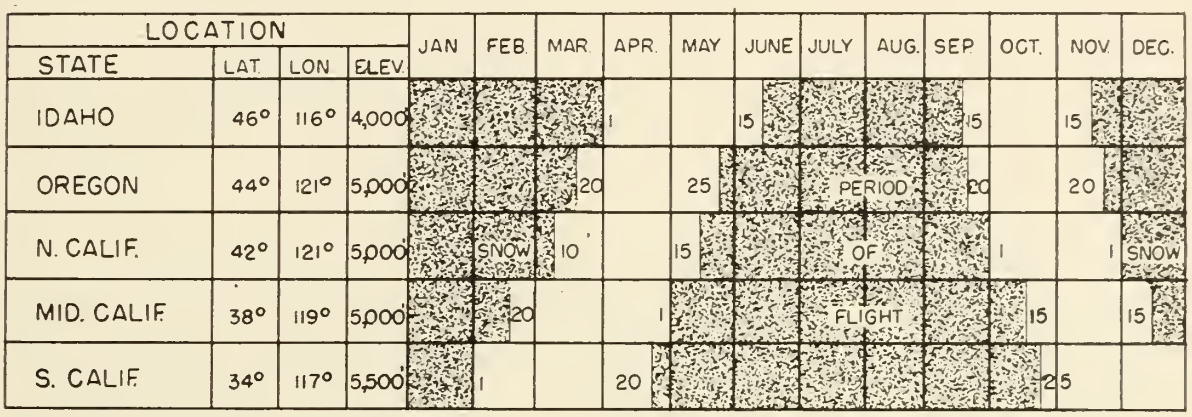

FIGURE 65.—Open seasons for western pine beetle control in ponderosa and Coulter pine.

areas. Western pine beetle broods can be destroyed at any time that infested trees can be found by methods suited to the season and conditions of the area. However, the cleanup of all infested trees within any large area can best be accomplished by fell-peel-burn during the dormant overwintering period. Keen (*61*) summarized in chart form the regional differences in periods when control on overwintering broods can be done to best advantage (fig. 65).

Keen also listed the advantages and disadvantages in control work during the fall, winter, spring, and summer working periods.

FALL CONTROL

ADVANTAGES	DISADVANTAGES
1. Destroys beetles in early stages before any emergence has occurred.	1. Infested trees difficult to find.
2. Some predators may escape destruction.	2. Bark hard to peel.
3. Fires progressively easier to control.	3. Shorter working season.
4. Easy transportation into camps over firm roads.	4. Camp may get caught in snowstorm, making it difficult to get out.

WINTER CONTROL

1. Destroys beetles before any emergence has occurred.	1. Infested trees difficult to find.
2. Permits covering larger area with seasonal work.	2. Bark hard to peel.
3. No danger of fires escaping.	3. Trees difficult to burn.
	4. Transportation difficult.
	5. Work interrupted by storms.
	6. Control work usually expensive.

SPRING CONTROL

1. Longer working period.
2. Infested trees easy to find.
3. Trees easy to peel.
4. Trees easy to burn.

1. Many beetles escape through early flight.
2. Work may be cut short by dry hot weather.
3. Fires progessively more difficult to control.
4. Ground soft and early transportation in control area difficult.

SUMMER CONTROL

1. Permits treating additional area or doing cleanup work on special projects.

1. Has failed to give satisfactory results.
2. Dangers from fires are great.
3. Solar-heat method not always effective.
4. Beetles in flight and only small percentage are destroyed.
5. Control work usually is expensive.
6. High percentage of predators are destroyed.

Types of Infested Trees Selected for Treatment

Broods of the western pine beetle rarely occupy all of the available bark surface of every infested tree on a control area. The infestation more often is mixed with that of engraver beetles, flatheads, or the mountain pine beetle in various combinations. Also, the broods of the western pine beetle are seldom found in a uniform stage of development. For overwintering populations, must of the broods are in the more advanced larval stages. But some infested trees contain only the first stage of attack, with parent adults and eggs in the phloem area. And other trees are partially abandoned, with only a few new adults remaining to comprise the straggling emergence of the main brood. Still further complications are set up when many trees in an area have only a small part of the upper boles infested. All trees of the above types must be classed as infested, since they contain some beetle populations.

Before instructions can be established for the spotting and treating of trees on any control project, it must be decided whether all types of infested trees are to be included or whether a selection is to be made of the more heavily infested trees. To kill the maximum number of beetles for the time and effort expended, it is often possible to accomplish more by concentrating work on trees with heavy broods and leaving untreated those trees that are only lightly infested.

Instructions issued to spotters and treaters on some projects have been much more detailed and specific than the above statement. For the large southern Oregon-northern California project, the instructions prepared by Keen (*U135*) included the following classifications:

Trees to be marked for treatment are those over 12 inches in diameter:

1. Containing live broods of the western pine beetle or the mountain pine beetle in the stage of larvae, pupae, or new adults (not more than 70 percent emerged) located within the project area and readily accessible.

2. Windfalls containing live broods of the above beetles.

Trees not to be marked for treatment are those:

1. Under 12 inches in diameter (unless in a group).
2. Showing only doubtful evidence of the western pine beetle or mountain pine beetle.
3. Partially attacked trees or those from which broods have completely or for the most part emerged (over 70 percent).
4. Trees abandoned in the top and infested for less than one log length at the base, or only on one side at the base.
5. Very remote from control operations so that their treatment would be excessively expensive.
6. Trees infested only with *Ips* beetles or flatheads.

The practices of selecting trees for treatment have varied with conditions in the different control projects. For the most part, tree-selection criteria have been defined by instructions issued to the spotters. Apparently, the practices followed on different projects were not arrived at through the results of adequate studies or tests. Instead they have been based on the experience and best judgment of entomologists connected with the projects.

In the early control projects, there was little selection among infested trees for treatment. One reason for this was that the cutting and peeling of all infested trees gave a fairly complete picture of the total infestation on an area, and the data thus obtained had a great deal of value in analyzing the entomological factors. In Hopping's (*49*) control manual issued in 1914, he specified treatment of "100 percent of the infested trees." This left little latitude for selection. The "Manual of Bark Beetle Control" by Keen (*61*) in 1927 recognized the advantages of selective treatment:

> Only trees with well-developed broods of beetles should be marked for treatment, and these before the trees have been two-thirds abandoned. In case of doubt as to whether or not the tree is heavily infested or has been partly abandoned, if a decision cannot be reached after a reasonable amount of inspection, a good rule is to mark the tree for treatment.

In the westside type of Sierra National Forest in 1931–32, another set of rules was used for the selection of trees to be treated. Here the problem was complicated by a very active California five-spined engraver infestation that initiated the first attack in the tops of a high percentage of the infested trees; this was followed by a western pine beetle attack in the lower bole. Gustafson (*U76*) used the following rules, which were drawn up by the Bureau of Entomology and Plant Quarantine:

I. *Trees to be marked for treatment:*

1. Western pine beetle brood at base regardless of color phase of of the foliage.
2. Green base, but with entire or most of crown fading, indicating that tree will die in any case.
3. Green base with foliage green or partially fading, but with pitch tubes or woodpecker work indicating western pine beetle attack in upper bole.

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4. Infested trees partially abandoned by the western pine beetle, but with more than 25 percent of brood remaining in the bark.
5. Sugar pines infested by the mountain pine beetle where these occur in the ponderosa pine type.

II. *Infested or faded trees not marked for treatment:*

1. Top-killed trees with less than 50 percent of crown faded and showing no indication of western pine beetle attack on the bole; these trees represent distinct top-killing by *Ips.*
2. Western pine beetle infested trees from which the greater part of the brood has emerged (less than 25 percent remaining in the bark).
3. Trees infested only by flathead at the base.

Differences in the instructions issued for these two projects can be explained by the widely different conditions in the two areas and the types of infestation. The southern Oregon-northern California project was located in eastside pine type with the primary infestations made up of the western pine and mountain pine beetles. The control effort was directed toward destroying as much as possible of the population during the limited control period; consequently, the instructions aimed to avoid dissipation of this effort in the treatment of doubtful or partially infested trees and in trees located in remote parts of the control area.

The Sierra project was characterized by a top-killing epidemic, followed by a buildup of western pine beetle in the top-killed trees. It was anticipated that the engraver beetle infestation would soon die out; the control effort, therefore, was directed toward destroying as high a percentage as possible of the western pine beetle broods in order to prevent further momentum of this infestation in the weakened top-killed trees. All trees containing western pine beetle broods were treated except those that were nearly abandoned. Engraver beetle infestations were not treated except when the broods occurred in trees infested by the western pine beetle. This strategy proved successful; the engraver beetle infestation disappeared the following year, and the western pine beetle was brought under control.

Hard and fast rules cannot be applied to the selection of trees to be treated; they must often be modified to meet special conditions in different areas, forest types, and regions. The entomological considerations involved in selecting infested trees are discussed in the following summary.

Western Pine Beetle

Advanced broods in the bark.—Trees are always treated when more than half of the bark surface is infested.

New attacks—parent adults and eggs in phloem area.—These trees have been treated on nearly all projects, although peeling and burning is difficult and the number of insects destroyed is small compared to trees with larval broods. However, if freshly attacked trees are left untreated, they are capable of developing broods to reinfest the area.

Partially abandoned trees.—These are usually left untreated if 75 percent or more of the brood has emerged. Even when the emergence is less than this, treatment is of questionable value because these

partially abandoned trees carry a very high number of insect predators.

Associated Insects

The California five-spined and Oregon pine engravers.—No special attention has been given to the treatment of engraver beetle infestations when these appear to be a minor or secondary factor. However, whenever engraver-killed trees or engraver-infested tops could be "thrown-in" with the treatment of western pine beetle trees without an undue amount of extra work, they have been included in the treatment. When engraver beetles have been an aggressive factor in the total infestation, groups of infested poles and single trees have been treated. (See "Top-killed trees," below.)

The mountain pine beetle.—The mountain pine beetle in ponderosa pine, a minor factor in western pine beetle infestation, is usually treated because it occurs in the same general bole area as the western pine beetle. Sugar pines infested by the mountain pine beetle are fairly common in the westside mixed conifer type. Nearly all control projects have followed the practice of treating infested sugar pines found in the same areas with western pine beetle in ponderosa pine.

California flatheaded borer.—In some areas, trees infested with flatheaded borers have been treated because they composed a high percentage of the total infestation and represented serious losses. For the most part, flathead infestations have been treated only when they occurred in the same trees with the western pine beetle. However, it is futile to attempt control of this borer by treating obviously dying trees. A large part of the stand may carry incipient flathead larvae in the cambium layer of green trees, ready to develop and kill their hosts whenever the hosts become sufficiently weakened. Until some new and more effective methods can be developed for the control of this flatheaded beetle, it should not be included in control plans.

Top-killed trees.—The question of what to do about top-killed trees has always been a difficult one to decide. The green basal part of the tree gives no indication as to whether the top was killed by engraver beetles, flatheads, or species of *Dendroctonus;* also there is nothing but the color of the foliage to indicate whether the tops are still infested or have been abandoned.

Rules for treating top-kills have been influenced by the fact that about 50 percent of recently top-killed ponderosa pine are attacked on the main bole by the western pine beetle within a few years. However, the remaining 50 percent may survive for long periods as stag-topped trees. Felling a top-killed tree for direct control involves considerable work in order to treat a small amount of infestation in the top; it also involves the risk of finding an abandoned top when the tree is felled. Consequently, the tendency on most projects has been to leave top-killed trees on the chance that they may survive.

A general rule has been to leave top-killed trees untreated if they have less than 50 percent of the crown faded, unless there is evidence to indicate that new attacks are advancing below the top-killed part. If more than 50 percent of the crown has faded and there is evidence that the dead part of the bole contains broods of the western pine beetle, the tree is felled and treated.

The Percent of Infestation To Be Treated

One of the first elements to consider in control planning is the intensity with which a control area is to be covered to find and treat infested trees. When the early western pine beetle projects were undertaken by the Forest Service, some misunderstanding developed regarding application of the "percentage principle" advocated by Hopkins (*44*). Apparently, it was assumed that 75-percent control meant that 25 percent of the infested trees that had been located on an area should be deliberately left untreated. Hopkins' explanation of the practice was stated as follows:

> The force should be directed to removing as large a percentage as possible of the infested bark from standing infested trees or from those felled for that purpose. The first work should be done in the principal areas and larger patches. *The work should be planned and executed with the object of destroying the greatest possible number of broods for the time and labor involved;* that is, if there are more infested trees than can be barked within the specified time, and 5 or 6 times as many insects can be killed by removing half of the infested bark from 3 to 4 trees as could be done in the same time by removing all of the infested bark from 1 tree, the former procedure is far preferable.

Hopkins' reasoning in advocating the leaving of some infestation in a control area seems to have been that 100-percent treatment would destroy all of the beneficial insects as well as the bark beetles; thus beetles coming in from the outside to reinfest the control area would find conditions quite favorable for a rapid increase of their numbers. Therefore, he thought some of the infestation should be left untreated either intentionally or otherwise in order to preserve enough beneficial insects to maintain the natural balance.

Hopping (*49*) made a very different interpretation of percentage control. In a control manual, he stated that in planning bark beetle control work, "the aim will be to treat 100 percent of the infested trees." In the same manual, he stated his belief that "bark beetles do not fly any great distance if trees of the species required by them are nearby." According to this reasoning, 100-percent treatment in a control area would eliminate the beetle population for a long time to come.

Results from the first western pine beetle control projects indicated that the difference between treating 75 or 100 percent of the infestation for the first year of control work was largely an academic issue. No matter how intensively the spotting and treating were done, some infestation always escaped. Even with the most careful and thorough work, it was difficult to find and treat much more than 75 percent of the total infestation. Infestations were hard to find in trees that did not show faded color when the area was spotted, in windfalls, and in the midbole of top-killed trees. Because of these concealed infestations, the practice was soon adopted of treating all of the infested trees that could be found: enough infestation would be missed anyway to take care of the percentage principle of control.

Checking the percentage of infested trees spotted at different seasons of the year in southern Oregon, Keen (*U136*) found that 63 percent of the summer generation trees were located by spotters in

summer control work; 76 percent of the trees harboring overwintering infestations were found in fall control work; 80 percent were found in winter control spotting; and 85 percent in spring spotting. During the subsequent summer's survey, 88 percent of the previous year's loss could be located. This showed that with the usual three-man spotting crew, about 12 percent of the infestation was inevitably missed. Keen also found no positive correlation between the percent of infestation treated and the subsequent reinfestation.

Recleaning of Control Areas

Although the factor of concealed infestation largely settled the issue of percentage control, there was continued controversy over the necessity for recleaning, i.e., the treatment of an area during the second and third years in order to eradicate infestation missed during the first year of control. On most projects a reinfestation of from 25 to 50 percent of the original volume developed the second year. Hopkins (*44*) considered it unnecessary to reclean an area after the initial control work had broken the force of the epidemic, because natural factors could be expected to take care of the remaining infestation. Hopping (*49*) disagreed with this:

> On the Barkhouse Project of the Klamath National Forest only 86.7 percent of the infested trees were cut and burned in 1912. The infestation is now nearly, or quite as bad as the original infestation before the initial control. Control work once begun must be followed up for at least three years to be effective, and after that must be followed by the regular administrative force and occasional trees cut and burned.

Begun in 1912, the first two western pine beetle control projects on Klamath National Forest are historically important because they represent the first effort to arrive at an understanding of the issues involved in the application of percentage control. The Craggy Mountain and Barkhouse units in the Klamath River watershed, containing about 15,000 and 20,000 acres respectively, were covered by fell-peel-burn control work in the spring of 1912.

Because these first large-scale projects were regarded as partly experimental, the Bureau of Entomology assumed responsibility for spotting the infested trees and supervising control methods. The policy followed on this initial work was to treat all that could be found of the 1911 overwintering infested trees. Later in the season, Hopping checked the Barkhouse unit and found that 86.7 percent of the overwintering infestation had been treated. It was estimated that a similar percentage had also been treated on the Craggy Mountain unit.

Although a reduction of about 60 percent in the volume of infestation could be attributed to the first year's control work, a considerable amount of reinfestation developed on both units during the 1912 season. It was then decided to reclean the Craggy Mountain unit and leave the Barkhouse unit untreated. This program was carried out in the spring of 1913, and no further control work was done on either area during succeeding years. Periodic surveys were made annually to determine the amount of infestation developing up to the close of the 1916 season.

Chief Forester Graves and others, inspecting the areas in April 1914, found that there had been a marked decline in the infestation during 1913 (later determined to be about 45 percent) on the Craggy unit after it had been recleaned. On the Barkhouse unit, which had not been recleaned, the decline had been even greater (later found to be about 65 percent). It was also found that the infestation had been reduced in both units to an endemic, nonaggressive condition. And the same endemic conditions were found in the adjoining area of McKinney Creek, which had never been treated.

The results up to April 1914 appeared to give ample support to the percentage principle advocated by Hopkins (*44*). The Chief Forester, therefore, prepared a statement to be attached to Hopping's (*49*) control manual in order to reconcile opposing viewpoints:

> The first aim of control . . . is to attack the points of concentration, striking the insects where they are most numerous. Because of the relationship between different parts of the infestation units, the destruction of large broods at concentrated points affects the rest of the infestation; and when the reduction of the insects in number has been carried to a certain point, the backbone of the infestation is broken and the insect attacks become scattered . . . This policy seems to be justified by the results on the Klamath Forest.

This conclusion was accepted until developments on these same two areas during succeeding years again confused the issue of percentage control. For the seasons of 1914, 1915, and 1916, the infestation in the Craggy Mountain unit continued in the endemic condition found in the spring of 1914. On the Barkhouse unit, a sudden increase of 249 percent occurred in 1915, followed by a decline of 53 percent in 1916. This 1915 increase on the Barkhouse unit paralleled a general epidemic condition that developed the same year in most of the watersheds of the Klamath and Rogue River areas. For some unexplained reason, this epidemic outbreak bypassed the Craggy Mountain unit.

These developments raised the question whether recleaning of the Craggy Mountain unit had been a factor in holding that infestation under control, while the Barkhouse unit, which had been treated only once, was subject to the same epidemic condition that prevailed in untreated areas in 1915 and 1916. But if the recleaning was effective in keeping the infestation under control, how often and how intensively is it necessary to rework an area in order to maintain satisfactory control and prevent epidemics?

As experience accumulated from other western pine beetle control projects, the controversy over the merits of percentage control was largely obscured by the practical considerations involved in its application. The core of the problem was not what percent of an infestation should be treated, but rather how much of it could be treated under varying conditions in area, types of infestation, timing of control, and different methods or eradication. If application of the principles required continued working of the same area year after year, then techniques adapted to maintenance control were needed. These had not been attempted in any of the earlier control projects.

After the Klamath projects, both Forest Service and Bureau of Entomology workers became interested in plans for an experimental

program to test methods and strategy for maintaining control over long periods of time. Plans for this experimental work were developed through a series of conferences at Ashland, Oreg., from 1917 to 1920 and were reported upon by Miller, Hopping, and Jaenicke (*U203*). These plans culminated in recommendations for the San Joaquin project, a 5-year program of experimental work to test the possibilities of maintenance control.

Maintenance Control

Maintenance control is based upon the idea that a small amount of control work at just the right time can prevent an infestation from developing into a serious epidemic. The big advantages of preventing the loss of timber and the high costs of epidemic control should justify the use of relatively expensive methods for maintenance control operations.

In his discussion of "How to Maintain Control," Hopkins (*44*) suggested that this work could be taken care of by rangers and fire wardens. He did not go into detail of procedure further than to specify: "It is not necessary that every isolated infested tree should be treated, but it is of especial importance that all groups of infested trees should receive prompt attention." Such considerations as status of infestation under which control should be undertaken, size of area which should be covered, timing of operations, results to be expected, and other practical problems to be encountered in the application of maintenance control were not touched upon by Hopkins. The San Joaquin project was the first attempt to find the answers to a number of questions that become important in considering the application of control under endemic rather than epidemic infestations.

Through the 5 years that it was in effect, the San Joaquin experiment explored a number of phases to determine (1) the methods best adapted to maintenance control, (2) the amount and value of the timber saved compared with the cost of control, (3) the possibility of reducing endemic infestations, and (4) the possibility of preventing epidemic increases.

The project was summarized by Miller (*U190*) in a final report entitled, "Control of the Western Pine Beetle on the San Joaquin Project." In condensed summary, Miller (*92*) says:

> An area of some 80,000 acres of yellow-pine type on the Sierra National Forest . . . was selected as the testing ground for the maintenance-control idea. For this type of forest the condition was regarded as epidemic, if the number of infested trees per section ranged 25 to 50. Control work had been carried out during the period from 1913 to 1917 on parts of the area where losses of this severity had existed. The experiment was planned with the idea of trying out various methods and systems of application and carefully following the course of the infestation not only on the control areas but also on selected check areas representing as nearly as possible the same type and conditions.
>
> In the five successive seasons during which this project was in progress the work was carried through three fairly distant phases:
>
> 1. A general working over of the entire area to make sure that the infestation was everywhere reduced to an endemic condition, or

an annual loss of 25 trees per section or less. This phase was completed in the spring of 1920.

2. Follow-up work, which consisted of a patrol of the entire area with small mobile crews of two or three men, and the treating of accessible trees as they could be found during the spring, summer, and fall periods. This work was planned so that the cost would not exceed 5 cents per acre. Its object was to detect increases as they were starting and to destroy enough of the broods to ward off incipient epidemics. Under this system less than 40 percent of the seasonal infestation was destroyed.

3. A comparison of the effectiveness of control when applied with varying degrees of intensity to small individual areas of 4,000 to 6,000 acres. This phase of the experiment varied from a conscious attempt to treat from 40 to 50 percent of the seasonal infestation by going over a unit once each season and treating only the overwintering broods, to an attempt at complete extermination by working throughout the entire season and treating every infested tree as soon as it could be found.

The results brought to light by this work emphasize the difficulties if not the impossibility of preventing insect epidemics by any direct control methods. Briefly stated, the project brought out the following:

1. Treatment of less than 40 percent of the seasonal infestation did not maintain control of the western pine beetle. On the area of 80,000 acres worked with this intensiveness the amount of infestation increased and decreased to the same extent as on check areas where there was no control work. The effects of artificial control were obscured by natural influences which caused the beetles to increase or decrease.

2. By the most intensive work with the object of exterminating beetle losses on an area of 3,600 acres, it was possible to treat about 90 percent of the total seasonal infestation. Failure to treat the remaining 10 percent was due to failure to find the broods in green trees which did not show discolored foliage until after emergence. Work of this character was effective in holding down an increasing infestation. During 1922, a season of general increase, the loss on the extermination area was 48 percent less than it was on the unworked checked area. However, during 1923, a year of natural decline, the reductions on the check area were appreciably as great as on the extermination area.

3. After control work was discontinued in 1924 a general increase occurred, and within one season the extermination area was reinfested to such an extent that losses on it were equal to those on the check area.

Conclusions drawn from the San Joaquin maintenance study can be summarized as follows:

(1) Continued maintenance control increases in relative costs and decreases in comparative effectiveness during a decreasing endemic infestation.

(2) Only very intensive maintenance work is capable of preventing an increase of infestation when the natural tendency is upward.

(3) The treatment of 100 percent of the infestation on a small area each year does not "exterminate" the beetles and is impracticable.

(4) In commercial pine areas, maintenance control by direct methods against endemic infestations is not warranted economically unless the treated trees can be utilized.

(5) In special areas where considerations fix a high value upon existing tree cover, maintenance control by direct methods can be justified.

The Devil's Garden Extermination Experiment

In 1928 a small isolated area of ponderosa pine type in Modoc National Forest, Calif., was selected for an intensive control experiment. One of the original purposes of this project was to determine the possibility of complete eradication of the western pine beetle in an area that was isolated on all sides from other infested areas by a continuous break in pine type.

The objectives of this experiment were originally defined by Keen (*U143*) as follows:

1. To stop beetle loss on this unit.
2. To determine the reduction due to control from 1, 2, and 3 successive treatments of an infestation uninfluenced by adjacent infested areas. This would take into account the reduction or increase due to natural causes by comparing the trend of this infestation with the nearest untreated areas.
3. After 2 seasons of control carried out as in commercial operations where the removal of 100 percent of the infestation is never realized, a third season of very intensive work would be undertaken to determine the possibility of complete extermination.
4. If extermination is secured, the area should be watched to determine in what manner an isolated area becomes re-infested. Will the beetles fly in quantities over a barren area of 6 miles, and if so are they able at once to kill standing trees, or must they first breed up in broken tops, windfalls, or other weakened material?
5. The area also lends itself to a complete study of the character of infestation present in every tree and a determination as to what extent trees may die without the agency of insects.

Plans for the project were set up by Keen (*U145*), and results were reported by Salman, (*U260*, *U267*) and Johnson (*U120*, *U121*, *122*). Control work began in the spring of 1929, and during the seasons of 1929 and 1930 all of the infested summer and winter brood trees that could be found were treated by the fell-peel-burn method. Thereafter the overwintering brood trees were thoroughly treated each spring up to and including the 1931 overwintering generation.

Although the western pine beetle infestation in the extermination area was greatly reduced during the control period 1929–32, the beetle was still present in the area in sufficient volume to be an important factor at the close of the 1932 season. Losses were still continuing in 1933, but by that time the California flatheaded borer had assumed the major role in the death of the trees.

In the final review of the experiment, Salman (*U260*) gave the following brief summary:

> Extermination of the western pine beetle was not secured. Flatheaded borer re-infestation may have come from within the area. Western pine beetle re-infestation, at least to a large extent, probably came from without the area. Control during 1929, 1930, 1931, and 1932 apparently did not reduce the losses markedly.

SOME RESULTS OF WESTERN PINE BEETLE CONTROL BY DIRECT METHODS

The greater part of control work against the western pine beetle has employed some direct method aimed primarily toward the reduction of beetle populations and prevention of further pine losses. Direct control methods have been used for so many years and on such a vast scale in the western pine region that it is now possible to analyze a number of projects and arrive at some conclusions as to the benefits that were obtained.

Control work from 1912 to 1952 involved hundreds of separate operations, varying in size from a few acres and a small number of infested trees to the 1.25-million-acre southern Oregon-northern California project. Some of these operations were designated officially as "projects" and special funds were appropriated for them; many of the smaller operations were considered as routine forest-protection jobs and were carried on by contributed labor. During the time of the Civilian Conservation Corps (1933–42), forest insect control was designated as part of the work program of many camps.

The greater part of the control work from 1912 to 1952 was accomplished by the fell-peel-burn method, supplemented to a limited extent by solar heat and oil treatment of infested bark. In its overall effect, this work undoubtedly resulted in the destruction of billions of beetles. An estimate of the actual saving of timber, however, has been attempted for only a limited number of projects where fairly complete records were maintained. Analyses of these projects are found in a series of manuscript reports.

Control in California, 1912–22

In 1922, J. M. Miller prepared a tabulated summary of all bark beetle control projects carried out in California up to and including the season of that year. This included 38 separate control operations varying widely in size of area and general infestation conditions. The smallest area contained 4,280 acres, the largest 69,400 acres. The majority of these projects were in mixed conifer type in which the western pine beetle made up the bulk of the bark beetle population, but with a minor infestation of the mountain pine beetle in sugar pine.

On about half of the projects, followup reports included an estimate of the reduction in board-foot volume of pine losses and comparisons of the losses for the year preceding and the year

following control work. On at least eight projects, these estimates were based on reliable examinations in the project areas (*105*). On the remainder, the results were either undetermind or estimated: Total number of projects, 38; area covered, 560,430 acres; trees treated, 25,242; board-foot volume treated, 29,015,000; total cost of control work, $102,492.

Results:	*Projects (number)*
Reduction of 50 percent or more of losses	14
Reduction of less than 50 percent of losses	3
Satisfactory reduction of losses	8
Temporary reduction of losses	1
Increase in losses following control work (40 percent)	1
No appraisal of results	11
	38

For the 17 projects reporting reductions by percentage in losses in the first year following control, the reductions ranged from 40 to 90 percent with an average of 64.5 percent. The general conclusion to be drawn from this summary is that substantial reductions of losses can be obtained by control work in the first year following the work. However, the factors that produced satisfactory results cannot be readily determined from the available data.

The Southern Oregon-Northern California Project, 1922–24

This project, the largest single undertaking of its kind, was planned to control a western pine beetle infestation over an entire timbered subregion of 1,276,000 acres (*58*). Practically all of the area included was eastside ponderosa pine type, with the western pine beetle predominant in the infestation. The total area was divided into three main theaters of operation, directed respectively by the Forest Service, the Indian Service, and private owners. The entire project was under technical supervision of the Bureau of Entomology of the U.S. Department of Agriculture.

The fell-peel-burn method was applied uniformly and with about the same efficiency throughout the entire project; therefore, it can be considered an adequate test of control work by this method. From January 1922 to the end of the project in 1924, treatment involved (*60*): Total area, 1,276,000 acres; area treated, 393,507 acres; trees treated, 31,512; board-foot volume treated, 35,006,000; total cost of control work, $144,880.32.

In 1925 Keen (*U138*) undertook an analytical appraisal of the results accomplished by the project. The basis for this appraisal was far more adequate than the one for the California projects, which had been carried out by different agencies under widely varying conditions. On the southern Oregon-northern California project, the conditions and the methods used were fairly uniform and a large series of check plots was maintained on which the pine losses were accurately measured. These check plots consisted of 29 treated sections (18,560 acres) and 30 untreated sections (19,200 acres).

The results of control work were determined by comparing the annual loss on treated and untreated sections for the years before and after control. This was done on the assumption that trend of

infestation was the same on both treated and untreated areas; hence, any differences in losses between the two areas was due to effects of the control work. On this basis, Keen found that between the years of 1922 and 1923 pine losses on the check sections decreased on the average of 16.4 percent, while on the treated sections the decrease averaged 43.9 percent. He considered, therefore, that the control work had resulted in a net reduction in loss of 27.4 percent. As an overall appraisal of the benefits of control work on this project, Keen stated:

> 1. The average net effect of control over and above any reduction from natural causes for the past two years has been to cause a 26 percent and 27 percent reduction respectively in the losses of the following year.
> 2. The reduction secured varied with the intensity of the infestation. With a loss of less than 65 trees per section (100 board-feet per acre) the effect of control was often totally obscured by the operation of natural factors. Above 65 trees per section reductions increased as the intensity of infestation increased. With losses of 250 trees per section (400 board-feet per acre), 48 percent reductions were secured by control.
> 3. Subsequent infestation depended to a considerable extent upon the amount of infestation left on the area.
> 4. When not obscured by the effect of other factors, the reductions secured were directly proportional to the amount treated, and in general for every tree treated approximately one less tree was killed the following year.

Keen also recognized differences in the results obtained according to the time of year when the work was done:

> From the results on the check sections as listed previously, we have the following comparison of the effect of spring and fall work:
> Spring work 1922—60 trees saved for every 100 trees treated.
> Spring work 1923—60 trees saved for every 100 trees treated.
> Fall work 1922—113 trees saved for every 100 trees treated.

The results of the fall work appear to be much better than those from spring work, especially the late spring work. The probable reasons for this are as follows:

> 1. The beetles in bark on felled trees which escaped the burning were either killed to some extent by molds and excessive moisture or, where the bark was on top of the logs or scattered on the ground, by the heat of the sun late in the spring before emergence.
> 2. The beetles in standing trees which escaped the treaters were to a large degree sought out and eaten by wood peckers during the winter when woodpeckers were forced to concentrate on the small number of missed trees for their food supply.
> 3. The odor of fresh cutting and burning was absorbed by the winter snows so that by the time of flight the attractive influence of the slash and the burning was negligible; thus avoiding any concentration of flying beetles into the treated area.

The results of this project also indicated that little could be gained by working an area over again the year following the initial control work:

Summarizing the results of nine sections treated in the spring of 1922, we find that following control the loss of 1921 was reduced from 1,165 trees to 815 trees, or a reduction of 31 percent. The next year the loss was reduced to 695 trees. This, however, is a reduction of 15 percent, while the natural reduction on all worked units averaged 16 percent. Therefore, following the first work, the units responded to the general decrease for the region.

Thus there was no additional reduction due to control, but the reduction which had been secured was simply maintained and the units otherwise responded to the natural factors which became operative.

Modoc Control Projects, 1931–32

The results from two fairly large control projects carried out against sharply increasing infestations within Modoc National Forest, Calif., during the winter and spring of 1932 were appraised by Salman (*U265*). The control phases of the two projects compare as follows:

Item:	*Badger project*	*White Horse project*
Period of control work	12/31–4/32	12/31–4/32
Total area treated, acres	19, 680	12, 140
Trees treated, number	1, 932	1, 027
Volume treated, M bd. ft	2, 345	1, 454
Cost of control, dollars	9, 478	3, 243

Salman appraised the effects of the control work as follows:

1. The control projects of 1931–32 in the Modoc National Forest were directed against a rising epidemic and took place during the first stage of the epidemic cycle.

2. The major effects of the two control projects, which in all projects appear in the year immediately following control, have been secured by cruises of actual losses on selected plots.

3. These cruises show that on the Badger control project area treated plot infestations decreased 5.8 percent in the year following control, while untreated plots showed an increase of 56.2 percent, a difference of 62 percent in favor of treatment. In the White Horse project area, treated plot losses dropped 42.8 percent and untreated plot losses increased 128.6 percent, a net difference of 170.8 percent in favor of treating.

4. Further favorable differential between treated and untreated plot losses occurred in the Badger area during the second season after treatment. Unfavorable differential occurred in the White Horse area in the second season, although it is believed the situation in 1933 represented a nearly normal condition.

5. The results show the benefit derived from treating an epidemic in its first stages, and when compared with results following the 1928–29 control, which was directed against a decreasing infestation, show the superiority of combating increasing epidemic infestations as a means of saving values.

Willow Springs and Badger Control Projects, 1934

These two projects were carried out in the eastside pine type of northeastern California during the winter and spring period of 1933–34. The two areas were quite similar in infestation types and general stand conditions, and the timing of control work and methods used were the same. The results, however, were quite divergent and illustrate the erratic response of western pine beetle infestations to the effects of control work.

In 1936 Salman (*U273*) compared the results obtained from these two projects. The data on which the appraisal was made consisted of accurate determinations of the annual loss on 5 treated plots (1,600 acres) and 13 untreated plots (4,160 acres).

Item:	*Project areas*	
	Willow Springs	*Badger*
Period of control work	12/33–5/34	12/33–5/34
Area covered, acres	23, 250	41, 345
Trees treated, number	4, 155	5, 848
Volume treated, bd. ft	3, 949, 000	5, 622, 640
Cost of control, dollars	18, 967	29, 487
Losses on control area:		
1st year after control	[1] **22. 9**	121. 3
2d year after control	**53. 6**	29. 0
Infestations on check areas:		
1st year after control	72. 3	94. 9
2d year after control	21. 1	115. 8

[1] Bold-face figures show a decrease in losses; roman figures, an increase.

Although the areas were treated for only one year, Salman apparently felt that the effects of control extended over 2 years.

The only favorable result that can be attributed to the Badger project is that during the second year after control, losses on the control area increased 29 percent while those on the check areas increased 115.8 percent. By applying this to the entire Badger project area, Salman estimated that 4,270,700 board feet of timber was saved as a result of control.

On the Willow Springs project, the control work showed a definite benefit. The volume of timber saved was estimated to be 10,500,000 board feet. In attempting to explain the widely divergent results obtained from the Badger and Willow Springs projects, Salman made the following comments:

> In both areas the infestations were increasing in 1933. In both the cycle reached its peak. Both included fringe areas and apparently similar environmental conditions. Composition of infestation was more mixed in the Lassen (Willow Creek) than in the Modoc (Badger) area, although in both areas species other than the western pine beetle were markedly active. Both areas were large, both bounded by timber on south, southwest, and east. Both were exposed to heavily infested timber within 20 miles on west and adjacent on east. Infestations were lighter to the south.
>
> We cannot put our finger on any particular factor responsible for the difference. It is possible that the lightly infested sparse stand south of the Willow Springs Project was a better barrier

than on the Modoc. It is possible that the continued attrition of environmental factors, or flathead borers or other insects, had reduced the level of resistance in the Modoc stands to a point much lower than on the Lassen.

California Region, 1931–36

During this period high epidemic losses occurred in both the eastside and westside pine types, and a large amount of control work was carried on by Federal and private agencies. The majority of the projects were financed through CCC and other emergency funds. The total program carried on during the period consisted of 41 separate projects covering a total of 560,000 acres at a cost of $327,000. Although most of this work was under the technical direction of the Bureau of Entomology and Plant Quarantine, administration of the control work and immediate field supervision were provided by the agencies conducting the projects.

Salman (*U273*) attempted to make an appraisal of the results of this series of projects. Since detailed data from annual loss inventories were available for only a few areas, however, the entire program could be appraised only in a general way. Salman first reviewed the projects according to the types of areas listed by Craighead, et al. (*26*) as representing the different conditions under which direct control work was considered to be entomologically sound.

	Projects (number)
1. Recreational areas:	
a. Small isolated areas	4
b. Areas with well-defined boundaries	10
2. Commercial timber stands:	
a. Eastside pine	12
b. Westside mixed conifer	15
Total	41

Salman quoted the following from Craighead, et al. (*26*):

> One season of thorough control work results in a reduction of western pine beetle losses on the treated areas as compared with similar untreated areas.
>
> The benefits have been greatest when the natural tendency of the infestation was upward.
>
> Under a declining infestation there was only a small difference in favor of the treated over the untreated areas.
>
> The benefits from control work have been temporary, lasting only one or two seasons, and a return to conditions similar to those on untreated areas can be expected unless work is continued on the same area year after year.

After comparing Craighead's conclusions concerning the results of direct control with the apparent overall results obtained on these projects, Salman summarized his own conclusions as follows:

> On the whole, it can be said that Craighead's general conclusions concerning the results of direct methods of forest insect control have been substantiated by recent experience. In addition, it may be stated that control of infestations at the peak of an infestation

cycle results in little or no saving of timber. However, the degree of control that is secured by one season's work against increasing or decreasing infestations is not always satisfactory. The fact that results are temporary and the limitation imposed by the economics of control under the present policy, all make it imperative that more consistently effective, more permanent and cheaper methods of forest insect control be secured.

Warm Springs Indian Reservation, Oreg., 1932–40

In 1940 Weaver (*U320*) made a survey of the Warm Springs Indian Reservation to evaluate the results obtained from seven consecutive seasons of western pine beetle control from 1932 through the 1940 season. This appraisal covered a total of 57,731 infested ponderosa pines with a volume of 37,149,000 board feet treated on 320,000 acres at a cost of $266,435. (The acreage includes the reworking of some areas covered more than once.) All of this work was carried on during the winter control seasons by the fell-peel-burn method.

Weaver analyzed the results of the work by a series of statistical tables, based largely on annual loss inventories on 11,767 acres in both treated and untreated areas. He based his general appraisal of the effects of control on what the predicted loss would have been if no control work had been done:

> Pine beetle control work conducted on the Warm Springs Reservation during the past seven years has resulted in the saving of 131 million board-feet of ponderosa pine. At the rate of $3 M board-feet the control work conducted has thus resulted in the saving of $393,000 in stumpage values. To effect this saving, $266,434.79 of I.E.C.W. and CCC I.D. funds have been expended.

Weaver also pointed out that the effects of control were most marked during those years when the total area of heavy infestation was adequately covered by the work. This he illustrated by means of a graph and by the following discussion:

> . . . The peel and burn control work has profoundly influenced the course of the beetle epidemic on the Warm Springs Reservation . . . However, the beneficial effects of the control work are always temporary and the tendency is for the infestation to resume its normal course. During the years 1934, 1935, and 1936 ample funds were available and almost all of the epidemically infested portions of the reservation were covered by control work. Subsequent to that date, however, the amount of funds available for such work has steadily declined, while at the same time the beetles have been on the natural increase.

BIOLOGICAL CONTROL

Entomologists are always seeking a less expensive and more permanent control for the western pine beetle. All the direct control methods require a large amount of labor, and the costs have been high in proportion to the benefits derived. It was only natural, therefore, that timber owners should expect entomologists to find

some way to exploit the biological factors that control the beetles in nature.

The first ideas along this line were suggested by the work of woodpeckers. That these birds feed upon bark beetle broods in infested trees was a matter of common observation on the early control projects. Men whose duties required the tedious peeling of infested bark sometimes advocated the establishment of a "woodpecker farm" to raise birds for liberation in infested areas.

Studies that were made on the feeding habits of woodpeckers indicated that these birds were undoubtedly beneficial but were not as effective as they appeared to be (see Section II, p. 91). At best they devoured only a limited percentage of western pine beetle broods, and they seemed to show a preference for the beneficial clerids. Hopkins (*44*) thought that birds could have little effect upon a bark beetle epidemic because they could not increase their numbers fast enough to handle the rapidly increasing beetle population. However, in the Engelmann spruce beetle epidemic in Colorado in the early 1950's, woodpeckers demonstrated their effectiveness as a natural control agent.

Many of the insect parasites and predators considered for bark beetle control are listed and described in Section II, pp. 90–91. Parasites of the western pine beetle were soon dismissed as a factor in control because of their relative scarcity in nature and the physical conditions that limit their effectiveness. However, the native insect predators of the western pine beetle seemed to offer some possibilities for biological control, and a considerable amount of study and experimentation was done to explore possibilities for the use of these insects. Some of these studies led to modification of direct control practices in order to protect the predators. And at least three methods have been proposed for protecting and increasing the insect predator population within an area.

Protecting Insect Predators Under the Fell-Peel-Burn Method

In 1923, the first studies on the biology of clerid predators brought to light the fact that many of the larvae migrate down the tree when mature and pupate in the bark around the base of the stump and in surrounding duff (*U233*, *U235*). After the discovery of this pupation habit, the fell-peel-burn method was modified to avoid burning of bark around the stump. This was first stated in 1927 by Keen (*61*):

> The fire line . . . should completely encircle the tree (after falling), but *exclude the stump*. This precaution is advisable since many predaceous insects pupate in the soil at the base of the trees containing advanced broods of the beetles; preventing the burning of the debris around the stumps can save these insects.

There is no record of any studies to determine the actual control effect upon western pine beetle populations when this precaution is taken, but it is obviously good practice and is generally followed wherever conditions permit.

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Protecting Clerids Where the Solar Heat Method is Used

Person (*113*) proposed a method for increasing the effectiveness of the clerid *Enoclerus lecontei* Wolc. as a predator upon western pine beetle broods in areas where the solar heat method of control can be used. His studies had shown that in unpeeled infested logs exposed to the hot sun, the clerid larvae migrated from the top to the shaded underside of the log and survived. The bark beetle broods, unable to move, were killed on the top but survived on the lower sides and bottom. When the log was turned, the clerids again migrated to the underside, but the bark beetle broods turned up to the sun were killed.

Person thought that if infested logs were exposed during hot weather and rolled three times so that each third of the circumference received direct exposure to the sun, then most of the pine beetle broods would be killed and most of the clerids would survive. In this way, the ratio of predators to beetles could be increased and the effects of predation multiplied. This proposed technique has never been tried because the solar heat method, effective only under very limited conditions, is rarely used on direct control projects.

Artificial Propagation of Predators

Interest in artificial propagation of predators for liberation in beetle infested areas was stimulated by the widely publicized success of biological control for a few agricultural pests. Forest entomologists, however, were not too optimistic over the feasibility or success of this method in the forest. The only predators available were native species, and their populations were maintained at as high a level as could be expected under natural conditions. The only apparent method of increasing these predators in a local area would be to rear them under insectary control, then liberate quantities of the adults. That nature's method of producing these insects could be improved upon by artificial techniques seemed questionable.

Forest entomologists at Berkeley decided to give artificial propagation of predators a trial in order to determine the practicability of the method and to work out obscure points in the predators' habits and food requirements. The project was undertaken with two of the most important predators of the mountain pine beetle, *Enoclerus sphegeus* F. and *Temnochila virescens* F. The clerid *E. sphegeus* is limited in its host selection and is found most commonly with the mountain pine beetle, but the ostomid *T. virescens* has a long list of insect hosts and is a very common predator of the western pine beetle. The experimental work was carried on at the Miami field laboratory by G. R. Struble during the seasons 1938 through 1941.

Struble began with the eggs of the predators, trying various methods of incubation and of feeding the larval stage through to pupae and adults. He used a number of food media, mostly insect larvae. The ostomid responded better to substitute foods, but the best development was obtained when bark beetle larvae were used. The greatest difficulty in rearing proved to be the cannibalistic habits of the predators, which made it necessary to rear them separately. Nor-

mal healthy adults were produced when predator larvae were kept in separate glass vials and fed frequently on larvae of the mountain pine beetle. A stock of mountain pine beetle broods for feeding the predators was maintained by infesting ponderosa pine logs in a screened insectary.

Struble (*127*) found that this successful technique of rearing required a considerable amount of labor and material, the cost of which averaged around $125 for 1,000 predators. In the report of these propagation experiments published in 1942, he concluded:

> Although mass production and greater improvements in methods of rearing through use of substitute hosts may greatly reduce this figure, it may still be much too high to be practical. The main reason for this is the necessity of handling each predator larva separately . . . The cost of rearing these predators by use of their native hosts as food is much too high for practical purposes. Furthermore, the set-up of logs in which to rear the host is too cumbersome and is wasteful of green timber . . . Unless methods can be developed which will overcome these objections, there is little hope of increasing the beneficial effects of these predators beyond that of protecting them in nature.

PREVENTIVE MEASURES

The possibilities of protecting individual trees from bark beetle attack have not been overlooked. The development of a protective spray or other means of saving individual trees could be of great service where pines are of special value as shade or ornamental trees. Many protective measures have been tried; so far, none have been completely successful.

Screening

Screening the trunks of individual trees with wire mesh to ward off the beetles was one of the first measures tried in preventing bark beetle attack. This has not been attempted with the western pine beetle, but according to Gibson (*U71*) it met with some success in preventing attack by the mountain pine beetle on lodgepole pines. Patterson (*U224*) also had success with screens in preventing attack on lodgepole pines at Crater Lake National Park in 1926. The method, however, seems to be impractical with the western pine beetle. It would require a finer mesh screen, and this would be quite difficult to install in the midbole and top of large ponderosa pines where the beetle usually starts its attack. In the case of lodgepole pine, it was necessary to screen only the lower 25 feet of the bole to prevent attack.

Tanglefoot

A sticky substance intended to trap adult beetles on the outer bark of trees was tested in 1937. Offered by a chemical spray company, this liquid tanglefoot was tried on logs under cage control and reported upon by Struble (*U301*). The hard-shelled beetles were able to plow through the sticky tanglefoot and enter the logs without

much difficulty. A very few dead beetles were found stuck upon the surface. Obviously, this material was designed to hold soft-bodied insects. The strong crawling habits of species of *Dendroctonus*, which enable them to work through the sticky pitch tubes, make it extremely doubtful that any tanglefoot compound could be developed to hold them.

Repellents

In 1931 Struble (*U296*) tried out several patented insecticides proposed by commercial firms as repellents against bark beetle attacks. The materials included flusi-dust (sodium fluosilicate), creosote emulsion, Bolite, paradichlorobenzene in linseed oil, and Thymol, all tested against the fir engraver beetle on white fir. The results of these experiments led to the conclusion: "The use of these chemicals by applying them externally does not seem justifiable because (1) the toxic or repellent effects do not last long enough, and (2) the mechanical composition of fir bark does not permit penetration to any appreciable depth." The same objections seem to apply to the use of these materials as repellents of the western pine beetle.

Experiments to find a specific repellent for the western pine beetle were taken up by Norman Gay of the Standard Oil Research Laboratory in 1932. Gay's tests were made by exposing green trap logs in the field and in cages with numbers of adult beetles. The materials tested were sprays consisting of (1) an asphalt emulsion that solidified on the bark surface forming a hard coating nearly one-fourth inch thick, (2) an oil-naphthalene mixture, and (3) an oil-Paris green mixture.

In all tests the beetles succeeded in boring through the materials on the outer bark and establishing attacks in the green phloem. If there was any repellent effect from the sprays, it was obviously overbalanced by the attraction of the green logs. Some beetles apparently were killed in making their attacks, but the fact that enough adults got through to completely infest the logs disqualified all of these materials as repellents or control agents.

Residual Sprays

With the availability after World War II of the newer, more potent residual insecticides such as DDT and BHC, the possibility of developing protective sprays was greatly increased.

Patterson (*U231*) found that engraver beetles could be prevented from attacking piled fresh slash for a period of 60 days (or until the slash dried out) by spraying thoroughly with a 5 percent DDT solution in diesel oil. Attempts to prevent attack by spraying standing trees were inconclusive, because none of the treated or untreated trees were attacked in the year of the experiment.

More recent experiments by Perry (*U232*) and Moore (*U213*) indicate that control of the western pine beetle with residual-type sprays may well be possible through systematic development of formulations and application techniques. Further work along this line is underway.

INDIRECT CONTROL THROUGH FOREST MANAGEMENT PRACTICES

From studies of ecological relationships (Section III) came the realization that attacks of the western pine beetle had caused the silvicultural practices used in ponderosa pine stands to become obsolete. Stands that contained a high percentage of mature slow-growing trees were found to be more susceptible to infestations than stands made up primarily of vigorously growing trees. Western pine beetle infestations were making periodic thinnings, which released trees from stagnation. The beetles attacked and killed the old susceptible veterans—suppressed, intermediate, codominant trees. The thinning made openings for regeneration, and thus stimulated the growth of young trees. The result was an uneven-aged forest composed of even-aged groups of trees. Moreover the beetles were determining the natural rotation of ponderosa pine on different sites (*72*, *74*, *80*). With these clues, foresters began developing a silvicultural system for ponderosa pine management that takes into account the natural habits of the tree and the part of the western pine beetle plays in its ecology.

The obvious approach to effective beetle control was through the use of silvicultural measures, conforming to the natural ecological pattern, which would maintain a healthy, resistant condition of trees in the reserve stands. Methods considered and tested include surface burning, stand improvement thinnings, selective logging, and a modified form of selective logging known as sanitation-salvage. None of these methods involve the killing of broods of beetles; they are, therefore, quite indirect in their control effects.

Surface Burning

The amount of ground cover consisting of brush and dense stands of reproduction is related to bark beetle hazard, Bedard (*U17*) pointed out in a study analyzing certain hazard factors in eastside pine stands. Weaver (*142*) also came to the conclusion that a heavy understory of pine poles and reproduction in pine stands growing under limited moisture conditions will result in severe competition with mature trees. Weaver felt that heavy depletion by bark beetles is inevitable unless the understory is thinned. Periodic light fires offer one way to thin an understory to the point where it will not deprive older trees of available soil moisture. Thus it has been argued that periodic controlled light burning will keep a merchantable stand in a resistant condition and act as an indirect control measure against the western pine beetle.

The beneficial effects of light surface fires in reducing bark beetle damage have been shown on a number of areas (Section III, p. 216). However, many disadvantages connected with the use of fire for beetle control must be taken into account. Considerable injury to growing stock may result from light burning, and this will increase bark beetle damage for a period of years. The enlargement of fire scars on mature trees will increase breakage and windthrow. This may reduce volumes to such an extent that many years of improved growth and lowered bark beetle damage will be needed to recoup these losses. The hazards and the objectionable silvicultural effects

involved in the use of light surface fires for reducing bark beetle damage will probably continue to preclude the adoption of burning as a control method.

Stand Improvement Thinnings

Stand improvement projects in the pine region have been designed primarily as silvicultural experiments; insect control considerations on such projects were entirely secondary. But on a number of thinning projects carried out during 1934 in California, forest insect developments resulting from the operations were followed. The chief entomological concern on these projects seems to have been the possibility that pine engravers and other bark beetles would develop in the slash, then attack in the green stand after the thinning. Salman (*U272*) summarized the results of the thinning projects and concluded:

> There does not appear to be any great hazard (of western pine beetle build up) created by cutting of small-sized reproduction and poles. A hazard does appear to be created by cutting large-sized material, particularly if it is felled in a group of trees of similar or large dimensions.

On the whole, the results of these preliminary improvement thinnings appear to have little application to western pine beetle control. The stands selected for treatment were made up largely of young trees that had not reached the diameters and ages that favor infestations.

Selective Logging

Control by selective logging is based upon the premise that trees vary in susceptibility to attack by beetles. If susceptible trees are removed, the residual stand will be made up of more resistant trees. The beetles then will find the nonsusceptible trees unfavorable for maintaining their populations; they will not be able to develop to epidemic proportion and cause serious losses. The entomological considerations in the application of this method of control are as follows: (1) Which are the susceptible trees? (2) How can susceptible trees be distinguished from resistant trees? (3) Is it necessary to remove all trees showing indications of susceptibility, or will removal of only the most highly susceptible trees suffice?

The basic factors underlying these questions are discussed under ecological relations of the western pine beetle (Section III, p. 139). In this section, we consider their application to selective logging practices.

Removal of the Slower Growing Trees

In the first attempt to use selective logging as a control measure, trees were selected for cutting almost entirely on the basis of growth rate. Person's (*111*) early work had pointed to reduced growth rate as the dominant factor in the choice of trees by the western pine beetle. This indicated a possibility of using reduced growth rate as an index in selecting trees for removal to reduce the beetle-caused loss. In 1929 an experiment to test this theory was undertaken on a 40-acre plot (Timber Mountain) where tree susceptibility had been studied (*U242*).

On 20 acres the trees that were considered to be susceptible were selectively logged, and the remaining 20 acres were left untreated to serve as a check. The experiment was described in two reports by Person (*U243*, *U247*). The trees were selected for cutting on the basis of radial growth of less than 1 mm. per year and the silvicultural requirements necessary to leave an adequate reserve. On the 20-acre treated plot, 53 percent of the susceptible trees (59 percent of the stand volume) were logged. Since it was not possible to remove all trees considered to be susceptible and still leave an appreciable reserve, only the trees of slowest growth were removed.

Progress reports on the selective logging experiment were prepared by Salman (*U261*), and Salman and Bacon (*U281*). The final results were summarized by Salman (*U266*), who concluded that the control was inconclusive because of the unfavorable conditions under which the test was conducted. The site was marginal, and the entire area surrounding the cutting plot was subjected to severe epidemic infestations for the 5-year period following logging. Salman stated:

> Under the environmental conditions affecting the stand included in this experiment, the cutting and removal of unthrifty and susceptible trees to the extent of 59.5 percent of the volume had not resulted in any marked reduction in the intensity of the infestation or saving of timber other than that utilized in the cutting operation.

Removal of Susceptible Trees by Classes

Indirect control through selective logging was measurably advanced by the development of tree classifications based on age and crown vigor (see Section III, p. 176). Keen (*68*) stated: "Once the type of tree most likely to be killed (by pine beetles) can be recognized with a fair degree of certainty, it is possible to make partial cuttings of beetle-susceptible trees, either for the purpose of salvaging valuable high-risk trees before they are damaged by beetle attack or for the silvicultural objective of reducing mortality and increasing net growth." Keen showed that 8 of his 16 tree classes, particularly those of C and D crowns, were of highest beetle risk, and suggested two types of cutting: (1) a salvage cut of 14.4 percent of volume limited to the 4C and 3C trees of highest risk and value, and (2) a preventive treatment taking all of the susceptible types and removing approximately 56.4 percent of the volume.

Keen's tree classification was first put into use in 1935 on the Edward Hines Lumber Company logging operation on the Silvies Working Circle of Malheur National Forest, Oreg., where the "maturity selection system" was being developed by Brandstrom (*8*). In 1936 the classification was also applied to an experimental "thrift selection" cut on this same working circle. In each case, a 40-percent cut of the stand volume was made.

This area provided the site for a study to compare the effect of these experimental light cuts on timber mortality from bark beetles with the effect of heavier standard Forest Service cutting practice and with mortality in nearby virgin uncut stands. The study was initiated in 1937 by the establishment of a series of six 320-acre plots in each of the three types of cutting and on the uncut stands. Whiteside (*U335*) summarized the loss records on these plots for the period 1937–44, and presented results of the study for the 8-year period.

The three "methods of cutting" used on adjoining areas of the Silvies Working Circle were defined by Whiteside (*U333*) as follows:

1. *Standard Forest Service 80-percent selection.* Cuts of approximately 75 to 80 percent of the pine volume were made in the older and least thrifty trees. The younger classes and at least one seed tree per acre were left. All snags were felled, and the slash was burned. This type of cutting was made during the 1930–35 period.

2. *Forty-percent economic or "value selection."* Trees to be cut were selected on the basis of the maturity selection rule of earnings. Considering growth, mortality, and earning rates, only trees that would net the operator at least $2.50 per M board-feet were marked for cutting. While value determined the selection, in some cases trees in Classes 3A and 3B were left as substitutes for lower valued trees in Classes 4C and 4D over 22 inches d.b.h. However, these substitutions were limited to not over 10 percent of the cut. This cutting was made during the 1935–38 period.

3. *Forty-percent silvicultural or "thrift" selection.* Rules for this type of cutting were applicable to trees in age Classes 3 and 4 provided that no trees under 22 inches d.b.h. would be taken. All age Class 4 trees above this diameter limit were to be cut unless needed for seed trees or to fill openings. No Class 3A trees were to be cut. Trees in Classes 3B and 3C were usually left unless they were undesirable as part of the reserve stand. Cutting was done during the 1936–39 period.

The study plots showed an immediate reduction in insect-caused loss for the first year after cutting. In the second and third years after cutting, there was a marked increase in losses probably due to the effect of logging disturbances. After the third year, the trend of losses dropped sharply each year to the sixth year, at which time losses were classed as low endemic.

The average annual gross mortality, including beetle-kill and windthrow over the 8-year period following cutting (7 years on the thrift plots) was as follows:

	Mortality per acre		*Gross mortality of stand*	
Plots:	*Insect caused (bd. ft.)*	*Total (bd. ft.)*	*Insect caused (pct.)*	*Total (pct.)*
Virgin	69	85	0. 43	0. 54
40-percent value cutting	53	55	. 55	. 57
40-percent thrift cutting	33	37	. 29	. 33
80-percent F.S. standard cutting	16	17	. 35	. 36

As expected, the heaviest cut resulted in the least subsequent board-foot loss. However, in proportion to the residual stand, the least insect-caused loss occurred on the "thrift" cutting where all susceptible trees above 22 inches d.b.h. had been removed. A somewhat higher loss occurred on the 80-percent cut, while the 40-percent "value" cut showed a loss in excess of that on virgin plots. This was due to the abundance of high-risk trees of low merchantability left in "value-cut" stands.

The western pine beetle accounted for about 72 percent of the recorded mortality, while 16 percent was attributed to windthrow. To explain why certain trees were killed by beetles, Whiteside (*U333*) noted that many trees on both virgin and cut-over plots

received injuries that predisposed them to attacks in 1943 and 1944. Of these, lightning-struck trees were the most numerous.

Growth studies were not available at the time of Whiteside's report to appraise the amount of release resulting from the different systems of cutting. However, it was found that the general trend on both cut-over and virgin plots was definitely upward after 1939 with the 1942 growth well above normal.

After 1936, light selection cuttings primarily designed to remove the more susceptible tree classes (but also taking into account merchantability) became the rule in cuttings on Forest Service and Indian Service lands and on some private holdings in eastern Oregon and Washington. The primary purpose of these operations was to lightly cut areas of high beetle hazard as quickly as possible in order to "beat the beetles" to the high-risk trees and also to harvest those trees of high value which might be lost (*87*).

Timber marking in the interior ponderosa pine type of the Pacific Northwest and elsewhere has continued to make use of Keen's ponderosa pine tree classification as a silvicultural tool wherever removal of beetle-susceptible trees is a primary consideration.

Sanitation-Salvage

A greater refinement in designation of high-risk trees was developed by Salman and Bongberg (*121*) for use in an experimental trial of beetle control at Blacks Mountain Experimental Forest in California. From this work the term "sanitation-salvage" came into general use to designate the selective removal of trees of high risk to beetle attack as a method of indirect bark beetle control.

Blacks Mountain Experimental Forest, Calif., 1937–44

The Blacks Mountain Experimental Forest served as the first pilot test of sanitation-salvage cutting for control of the western pine beetle. This area, located in Lassen County, Calif., and comprising nearly 10,000 acres of eastside ponderosa and Jeffrey pine, is managed by the Pacific Southwest (formerly California) Forest and Range Experiment Station to test the practical value of theories of management, silviculture, and insect control for this forest type.

When management plans were first formulated for the area in 1933, there were heavy infestations of the western pine beetle in evidence. These were treated by the fell-peel-burn method in 1934. Timber losses were reduced by direct control and natural factors from an average of 202 board feet annually during the 1933–36 period to 73 board feet per acre in 1937.

The application of sanitation-salvage cutting for the removal of high-risk trees as a measure to reduce insect-caused loss was first employed on the experimental area in 1937, according to Bongberg (*U25*). During that season 322 acres were cut. In the following 7 years a series of compartments was cut each year until 3,100 acres of the ponderosa pine type had been covered.

Under this sanitation-salvage cutting program, all high-risk trees (Risk 4 and Risk 3) were removed. Where necessary for economic reasons, additional trees were added to bring the total cut up to about 2,500 board feet per acre. The sanitation-salvage cut amounted to 15.7 percent of the green stand volume.

The first results on this experimental forest yielded highly satisfactory control of western pine beetle infestations. Bongberg (*U25*) reported that:

> The comparison of loss conditions between treated and untreated areas has shown that as a result of cutting, losses were reduced the first year by 91 percent. Two years of loss subsequent to the cutting was 82 percent less on the treated area. For the three-year period, loss reduction has been estimated at 72 percent.

During the course of this project, a series of progress reports was issued including one report by Johnson (*U126*) that reviewed the results during the period 1937–43. High-risk trees were cut on a series of small selected compartments, with one or more compartments cut annually. This made it difficult to compute the control benefits, since the base of comparison between treated and untreated areas changed each year. The method adopted by Johnson and used later by Bongberg (*U34*) was to determine the natural trend of infestation on all untreated areas, then apply this trend to the treated areas.

In this way, it was possible to compute the losses that would have occurred if these treated areas had not been cut, but had followed instead the same natural trend as untreated areas. Thus if the normal trend was downward and untreated areas dropped 50 percent in loss between 2 years, the cut areas would need to drop at least 50 percent in loss before any control benefits could be counted. The natural trend of bark beetle infestation in the virgin stands of Blacks Mountain Experimental Forest from 1934 to 1947 (during the progress of these sanitation-salvage experiments) is shown in figure 66.

FIGURE 66.—Trend of bark beetle infestations in virgin stands, Blacks Mountain Experimental Forest, Calif., 1934–47.

At the end of 10 years, Bongberg (*U34*) reported the results from this sanitation-salvage cutting as follows:

Reduction in beetle-caused pine mortality

Annual basis (percent)		*Cumulative basis (percent)*	
1st year	86. 1	1 year	86. 1
2d year	87. 6	2 years	86. 8
3d year	91. 8	3 years	87. 8
4th year	87. 7	4 years	88. 2
5th year	87. 0	5 years	87. 8
6th year	83. 9	6 years	88. 1
7th year	86. 2	7 years	88. 3
8th year	76. 9	8 years	88. 8
9th year	74. 8	9 years	86. 9
10th year	66. 7	10 years	70. 7

Summary of operation

1. Average volume of Risk 3 and Risk 4 trees cut, 2,680 bd. ft. per acre.
2. Average percent of total merchantable green stand cut, 15.7 percent.
3. Subsequent loss on cut area, 1937–46, 106 bd. ft. per acre.
4. Expected loss if area had not been cut, 601 bd. ft. per acre.
5. Volume of timber saved on cut area, 495 bd. ft. per acre.
6. Reduction in loss over 10-year period, 82.4 percent.

The cumulative control benefits of the Blacks Mountain project are represented in figure 67. This graph shows that a total of 495 board feet per acre was saved over the 10-year period 1938–47.

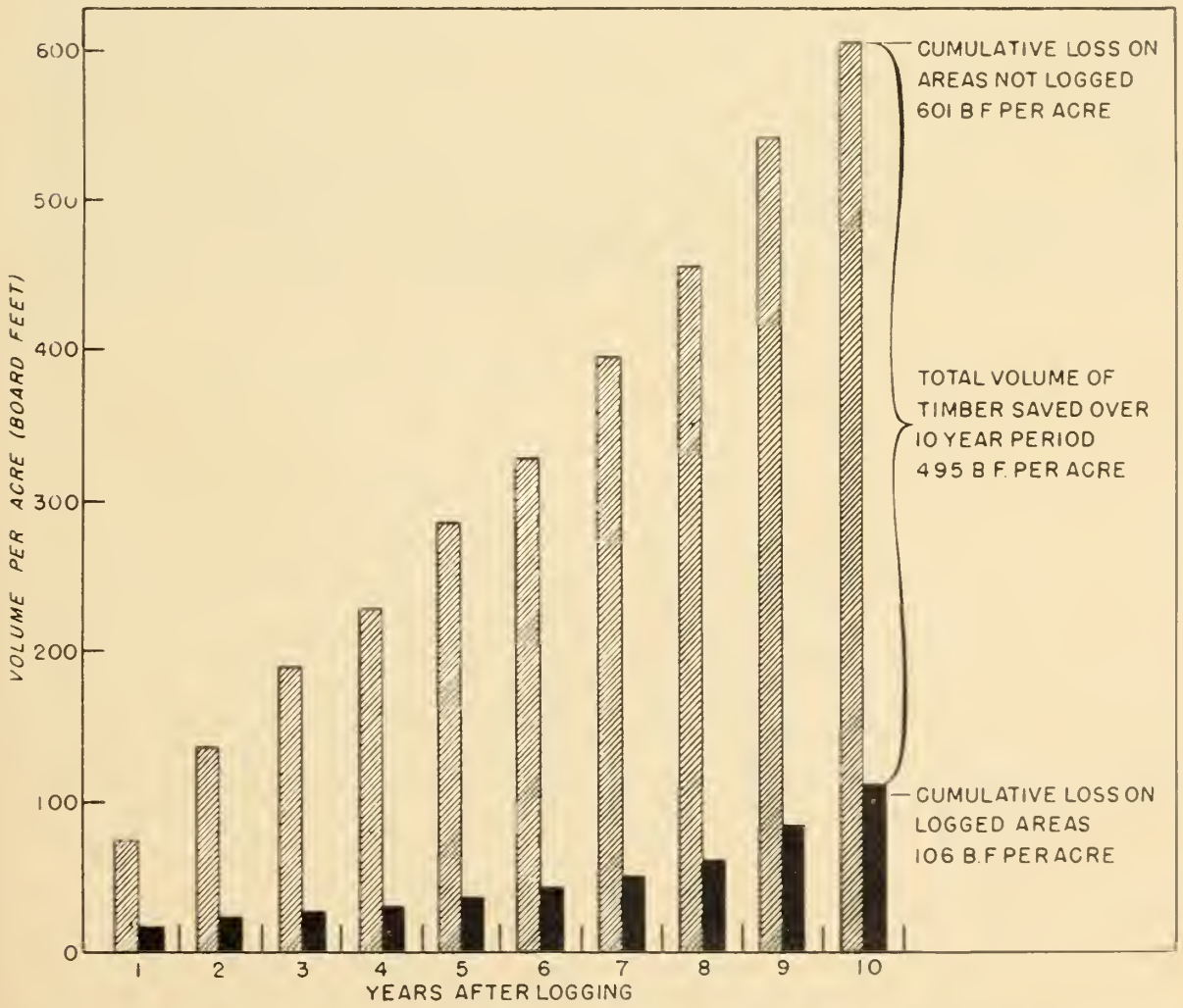

FIGURE 67.—Volume of pine timber saved during a 10-year period following logging of high-risk trees. Blacks Mountain Experimental Forest, Calif., 1938–47.

Bongberg (*U34*) concludes:

> Control results have far exceeded original expectations. Lasting benefits for periods up to 10 years are believed due to an upsetting of the normal ecological balance between the bark beetles and the host tree. Control results are conclusive evidence that sanitation-salvage logging is highly effective as a measure to be used for bark-beetle control in interior type ponderosa and Jeffrey pine stands.

Dixie Valley Sale Area, Plumas National Forest, Calif., 1940

Following the demonstration of sanitation-salvage and its effectiveness on the Blacks Mountain project, the Forest Service decided to test the practicability of the method where bark beetle control was needed on timber-sale areas in other eastside pine types. The Dixie Valley sale area on Plumas National Forest was selected. Because of sustained beetle losses, a tract of 8,000 acres was advertised for light selective logging in 1940. The Forest Service agreed to mark for cutting not less than 25 percent of the green merchantable stand, about 50 percent of which was Jeffrey pine.

While the crown characters indicative of high risk in Jeffrey pine were similar to those in ponderosa pine, a new biological element was introduced in this project because of the prevalence of a Jeffrey pine beetle infestation. According to Bongberg (*U26*), who described the operation, "The chance to determine the effectiveness of this light treatment on areas predominantly Jeffrey pine was important, since there were some indications that the Jeffrey pine beetle showed preferences in host selection unlike that of the western pine beetle in ponderosa pine."

It was estimated that about 15 percent of the green stand was made up of high-risk trees. In order to provide the minimum cut of 25 percent guaranteed to the logging company, it was necessary to supplement the high-risk cut with other trees considered to be undesirable from a silvicultural standpoint. The entire Dixie Valley area was logged by sanitation-salvage methods in 1941 with an average cut of about 3,500 board feet per acre or 26 to 31 percent of the stand.

Ponderosa pine loss was reduced by nearly 100 percent, Jeffrey pine loss by about 82 percent in the first year after cutting. The costs of logging averaged 25 percent higher than for a heavier cut because of the amount of road construction and the relatively light yield per acre. This cost factor was not entirely satisfactory for the logging company. The timber was federally owned, therefore the company received no benefits from protection of the reserve stand.

In 1942 the Forst Service undertook other sanitation-salvage sales on Modoc and Lassen National Forests in California, and in subsequent years rapidly extended the principle of sanitation-salvage to many other areas in eastside types (*U28*).

Cayton Valley Sanitation-Salvage Cutting, 1939

Some private timber owners were not long in recognizing that beetle control by sanitation-salvage methods was preferable to direct control. This indirect method of control paid its way through the utilization of timber that would otherwise be lost. In addition, sanitation-salvage cuttings were more effective in reducing losses.

The first sanitation-salvage control operation by a private company was started by the McCloud River Lumber Company in 1939 on a tract of 1,440 acres in Cayton Valley, Shasta County, Calif. Another test was made by the same company in 1940 on 600 acres in the Harris Mountain tract. The purpose of these cuttings was to obtain protection from beetle-caused losses over a 5-year period, after which these stands were expected to be cut over in a regular logging program. The company also was interested in determining the costs of this indirect method of control as compared with the direct methods that they had been using for many years.

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FIGURE 68.—Mobile loading rig mounted on a tractor, developed by the McCloud River Lumber Company for sanitation-salvage logging in Cayton Valley, Calif.

Special mobile loading and trucking equipment was purchased by the company for the operation with the expectation that it would be used in further sanitation-salvage operations (fig. 68). Only trees of highest immediate risk (Risk 4) were marked for cutting. This resulted in a very light cut averaging about 600 board feet per acre.

Forest entomologists cooperated with the company in this experiment by indicating the trees to be cut and by studying the results as shown by sample plots (*U29*). Bongberg (*6*) reviewed the results of this test during 1939 and for the five subsequent seasons.

Summary of operation

1. Volume or risk trees cut (Risk 4 only), 563 bd. ft. per acre.
2. Percent of green stand volume cut, 8.5 percent.
3. Subsequent cumulative loss on cut area (1940–45), 81 bd. ft. per acre.
4. Subsequent cumulative loss on adjacent uncut areas, 529 bd. ft. per acre.
5. Savings resulting from operation, 448 bd. ft. per acre.
6. Average annual reduction in loss, 84.7 percent.

It was estimated that the 448 board feet per acre saved for harvest at the end of the 5-year protection period more than offset the increased logging costs entailed by this light selective cut. The sanitation-salvage operation therefore paid for itself. Had fell-peel-burn methods been used, an outlay of funds would have been necessary for the treatment of infested trees, very few of which could have been salvaged to defray control costs.

Rail Glade Area, Bly District, Klamath County, Oreg., 1940

In 1940, the Weyerhaeuser Timber Company began a test of sanitation-salvage on the Rail Glade area, 960 acres located in the lower margin of the ponderosa pine type surrounding the Sprague River Valley near Bly, Oreg. An 18-year record of beetle-caused losses on this area showed an average annual mortality rate of 1.7 percent of stand volume. The prospect was that loss rates would continue to be high unless some action were taken to reduce them.

Forest entomologists assisted with the planning and selecting of trees to be cut, while Thomas J. Orr, Jr., forester for the Weyerhaeuser Timber Company at Klamath Falls, directed the logging. The planning, initial phases, and results of this test for the first 2 years were reported by Keen (*U155, U159, U162*). Bedard (*U18*) reported the third year's results, and Bongberg reported the fourth and fifth years' (*31*) and the final results (*U35*).

The marking rule developed by Keen and Orr for this particular test integrated considerations of risk (current health), tree class, and value. First consideration was given to risk rating, second to Keen Tree Class, and third to value.

Synopsis of marking rule

Risk 4. Very high risk; all cut.	Cut all classes except age class 1.	Cut all positive value trees; cut negative value trees down to 12 inches if in groups and likely to contaminate valuable trees.
Risk 3. High risk; partly cut.	Cut susceptible classes in C and D and 4B trees if of declining vigor (—) except age class 1.	Cut some trees of normal vigor, in susceptible tree classes, if of high value.
Risk 2. Fairly healthy trees; moderate risk; none cut.	None cut even if of slightly declining vigor (—).	Not even high value trees in susceptible tree classes cut.
Risk 1. Healthy trees; low risk; none cut.	None cut	Do.

In addition to the above, spike-top trees were cut if they showed signs of active insect work in the crown below the spike top. Trees forking from a common stump were both taken if one of them was a risk tree. Cull trees were cut from groups and dragged out into openings 50 feet away so they would not attract beetles into the group.

The cutting in 1940 covered 780 acres from which 895,380 board feet of high-risk trees were removed. This represented a cut of 1,150 board feet per acre, or approximately 18 percent of the total green stand.

The final results of this test, reported by Bongberg (*U35*), indicated yearly reductions in loss as compared with the losses on uncut areas.

Year following cutting:	*Mortality reduction* (*pct.*)	*Volume of mortality* *Assumed* [1] (*bd. ft.*)	*Actual* (*bd. ft.*)
1st	94. 2	99, 500	5, 790
2d	72. 3	48, 800	13, 510
3d	70. 7	29, 600	8, 680
4th	73. 4	39, 900	10, 610
5th	84. 6	43, 700	6, 750
6th	88. 2	41, 000	4, 820
Total	----------	302, 500	50, 160
Average for 6-year period	83. 5	50, 417	8, 293

[1] If no control had been done and natural trend followed.

Summary of operation

1. Volume of risk trees cut, 1940, 1,150 bd. ft. per acre.
2. Percent of stand volume cut, 18 percent.
3. Subsequent loss on cut area, 1940-45, 64 bd. ft. per acre.
4. Expected loss if area had not been cut, 388 bd. ft. per acre.
5. Volume of timber saved on cut area, 324 bd. ft. per acre.
6. Average reduction in pine losses over period, 83.5 percent.

Bongberg concludes: "Final results of the experimental test of pine beetle control through sanitation-salvage logging proved to be highly satisfactory for a period of 6 years. All objectives of the test were met and the reserve stand was protected against excessive beetle-caused mortality until harvested during 1946."

Swede Cabin Area, Bly District, Oreg., 1941

The Swede Cabin operation was the second step in the development of a sanitation-salvage program by the Weyerhaeuser Timber Company. Having learned from the Rail Glade pilot test that this method increased the cost of log production only slightly, the company expanded the treatment to extensive holdings in the eastside pine type. This expanded program was started in 1941 on a 6,000-acre tract of the Sprague River drainage near Bly, Oreg., known as the Swede Cabin area.

The Swede Cabin area contained a highly susceptible stand of ponderosa pine, as indicated by the fact that bark beetles had killed 12.4 percent of the original stand estimated at 18,000 board feet per acre during the period 1930–40.

As reported by Bedard (*U19*), the rule for selecting trees to be cut on this area was essentially the same as that used on the Rail Glade area the previous year:

> The exceptions were that negative value trees were not taken, badly leaning trees were taken, and the double root-crown principle was extended to include trees growing within 18 inches of each other. In addition, a special effort was made to thin groups and eliminate all possible high-risk or so-called 'key trees' which might cause the entire group to be killed.
>
> In training the marking crew, the Tree Class Slide Rule and standard criteria for recognizing value were available to assist in securing uniformity in using these portions of the marking rule.

In addition, the penalty system of rating risk (see Section IV, p. 188) was put into operation for the first time.

Approximately 3,453 acres were logged during 1941, and 5,918 trees containing 5,621,200 board feet were removed. The cut was at the rate of about 1,630 board feet per acre or 10.3 percent of the stand volume.

Results of the Swede Cabin operation were reported by Bongberg (*U36*). The benefits derived from this operation are shown on an annual basis in percent of loss reduction in figure 70, p. 347.

Summary of operation

1. Volume of risk trees cut, 1,630 bd. ft. per acre.
2. Percent of stand volume cut, 14.1 percent.
3. Subsequent loss on cut area, 1941–47, 110 bd. ft. per acre.
4. Subsequent loss on untreated virgin area, 387.7 bd. ft. per acre.
5. Volume of timber saved on cut area, 277.7 bd. ft. per acre.
6. Average reduction in pine losses over period, 71.5 percent.

Bongberg concluded: "The reduction in beetle-caused mortality which has been afforded by this cutting has been highly satisfactory for the 7 years which have now elapsed since cutting."

The Rail Glade and Swede Cabin sanitation-salvage operations were reported upon by Thomas J. Orr, Jr., forester for the Weyerhaeuser Timber Company (*103*), who showed that the increased cost of logging on this light selection cut basis was between $1.50 and $2.25 per thousand feet. This expense could be offset by the value of the timber saved over a period of 5 or 6 years. Orr reported that "logs coming from a salvage operation will yield more No. 2 Shop and better and more Box than the average log of the same stand, but less of the higher common grades. This yield is, of course, the characteristic of mature timber and the actual difference in dollar value is slight."

Following these trials, the Weyerhaeuser Timber Company adopted a partial cutting program on all holdings in Klamath and Lake Counties, Oreg., (*104*). Selection of trees to be cut was defined in terms of Keen's age and vigor classes, to which were added the classes of current health developed by Salman and Bongberg (*121*). Selection of the younger half of Keen's Class 3 (mature) to be retained was determined by use of the tree class slide rule (*73*). The object of the marking was to leave in reserve the high-producing trees making the best growth. Up to 1945, more than 200 million board feet of timber was marked for cutting under this system. The results have been to leave a thrifty residual stand, in which losses have been negligible and the growth rate high.

Pringle Falls Experimental Forest, Oreg., 1950

In an extension of the concept of sanitation-salvage cutting into central Oregon's ponderosa pine forests, the Forest Service carried out an additional trial of this method of beetle control on Pringle Falls Experimental Forest near LaPine, Oreg., in 1950. The objectives of cutting, as stated by Sowder (*122*) were:

1. Remove live trees highly susceptible to insect attack and thereby reduce current and future insect losses.

2. Remove merchantable trees that are dead or dying from all causes and thereby salvage timber that would otherwise be lost.

3. Establish a permanent road system to facilitate future salvage or other cutting operations.

4. Reduce fire hazard and aid fire control.

A "penalty system" of rating risk, devised by Bongberg in collaboration with T. J. Orr and C. Borsting of the Weyerhaeuser Timber Company in 1948, was used (with some modifications by Sowder) as a basis for tree selection (table 8, p. 192). Trees with a penalty score of nine or more were considered as high risk and were marked for cutting.

The cutting was applied to 3,020 acres, removing an average of 1.2 high-risk ponderosa pine trees per acre with 1,606 board feet or 9 percent of the total pine volume. Returns of $24.29 per thousand board feet were received, and the total logging cost, including road construction, averaged $23.07 per thousand board feet. Sowder estimated that this cutting would produce a net gain, due to growth, of $1.07 per acre per year over the next 10 years.

Inland Empire

Johnson (*57*) assumed that the same principles of risk rating and sanitation-salvage cutting might be successfully applied to ponderosa pine stands of the Inland Empire. Cruises of mature ponderosa pine stands in the Kootenai River and Fisher River areas of Montana showed that the risk element averaged between 12 and 17 percent of the stand volume, comparable to the 16 percent found at Blacks Mountain in California. Sanitation-salvage cuttings have been carried out in the Inland Empire region, but results are not yet available.

General Results

All trials of sanitation-salvage show it to be an effective measure for reducing mortality for periods up to 10 years or more in eastside ponderosa pine stands subject to attack by the western pine beetle and in Jeffrey pine stands subject to attack by the Jeffrey pine beetle. Reducing losses is a most effective measure for increasing net growth. The principle of removing high-risk beetle-susceptible ponderosa pines as a first cut has now been generally adopted through the interior ponderosa pine type of California, Oregon, Washington, and Idaho (*1*).

There are, however, certain qualifications that limit the applicability of the method:

1. The highly favorable control results have been obtained only in the mature, slow-growing ponderosa pine stands of the eastside type. The adaptability of the method to the more thrifty westside pine stands is still in question and requires further study.

2. Sanitation-salvage does not apply to other parts of the ponderosa pine region, where such aggressive bark beetles as the Black Hills beetle or the mountain pine beetle are dominant.

3. This method does not apply to other timber species or to the control of other insects. The applicability of sanitation-salvage as an

insect control measure will have to be determined specifically for each insect and host.

4. The period during which sanitation-salvage cutting has been under trial has been characterized by low endemic infestations, and it is yet to be proved that it will maintain control under the impact of aggressive epidemic bark beetle infestations.

5. The use of sanitation-salvage is limited by a number of physical factors such as terrain, roads, and other transportation developments, and by the availability of mill facilities for converting the susceptible trees into lumber (fig. 69).

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FIGURE 69.—A load of logs from a sanitation-salvage cutting being hauled out of the forest.

6. Because sanitation-salvage requires the removal of such a high percentage of risk trees which could be expected to survive for 10 years or more (up to 85 percent of Risk 3 and 4), it is not appropriate for parks or recreational areas where the emphasis is on retaining trees for their aesthetic value rather than removing them for their present economic value.

Differences Between Areas in Results of Sanitation-Salvage

All of the sanitation-salvage tests described in recent reports show highly favorable control benefits over periods from 1 to 10 years. However, there are noticeable differences between areas in the behavior of bark beetle infestations following cutting and in the degree of control effects that were achieved.

The comparative benefits from the Blacks Mountain and Swede Cabin sanitation-salvage operations, figured for each area on the basis of the percent of reduction in pine losses compared with losses on

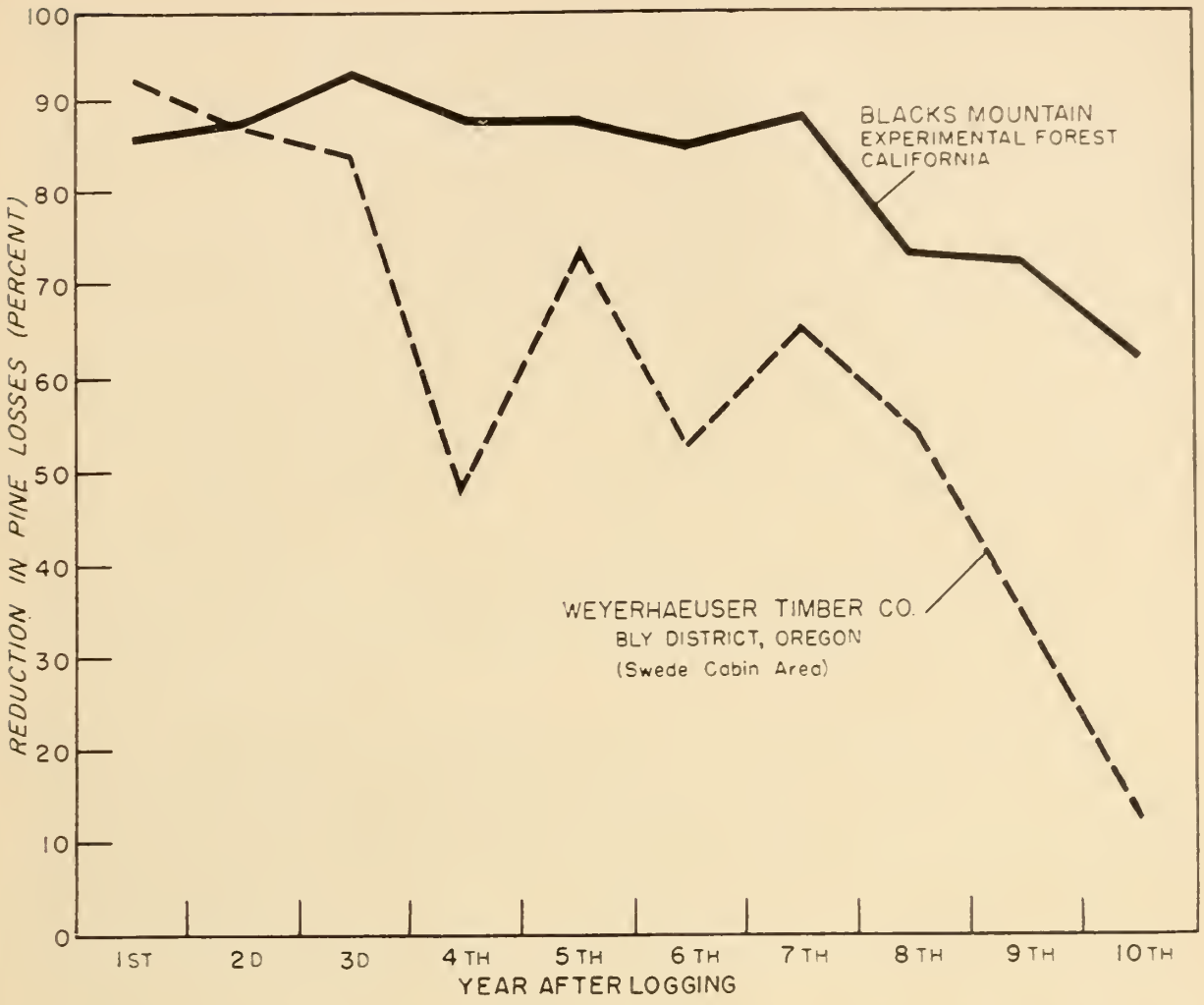

FIGURE 70.—Comparison of two projects in eastside pine type showing variable results in bark beetle control from logging high-risk trees.

adjacent untreated areas, are shown in figure 70. The Blacks Mountain treatment was most effective, showing approximately 85-percent reduction in losses for the first 7 years and a gradual reduction through the tenth year. The Swede Cabin area showed a similar high degree of loss reduction for the first 3 years, then an erratic pattern of loss reduction through the seventh year and a rapid reduction through the tenth year. The reasons for these differences between areas is obscure. They may be caused by differences in the rate of deterioration of mature pine stands, seasonal climatic conditions, the influence of surrounding beetle infestation such as windfalls, or other factors that act to modify the results of sanitation-salvage control.

Benefits Obtained by Direct and Indirect Methods of Bark Beetle Control

Bark beetle control work in the Burney area during the winter of 1946 provided the first opportunity to compare the results of direct and indirect methods in the eastside ponderosa pine type under almost identical conditions of site, climatic factors, and the infestation cycle. Work was conducted in the Burney Flat unit, an area of 27,700 acres located mostly north and east of the town of Burney, Shasta County, Calif.

A serious outbreak of Oregon pine and California five-spined engravers occurred in this area during the summer of 1944, followed by an increasing western pine beetle infestation during the fall. This outbreak was brought under control by the fell-peel-burn method during the late winter and spring of 1945 (*U85*). Following this initial control work in 1945, an endemic infestation of the western pine beetle still persisted in most of the control unit. State and private owners felt that direct control should be continued on a maintenance basis to protect the results achieved by the initial control work. On the other hand, forest entomologists recommended a sanitation-salvage cutting because experience in previous projects had indicated that direct control would not have much effect in reducing an endemic infestation of this kind. The program finally decided upon included the following phases:

1. Treat by direct fell-peel-burn method the western pine beetle infestation on areas treated the previous year. This was intended primarily as a maintenance control program.
2. Initiate sanitation-salvage on areas that had not been given the benefit of any previous treatment.
3. Establish a protection zone around Burney Falls State Park by the selective removal of high-risk trees, plus the fell-peel-burn treatment of infested unmerchantable trees, cull logs, butts, and tops. This treatment was termed "modified sanitation-salvage."

The 1946 operation provided an excellent test of the effectiveness of the three different control methods. Therefore, a series of half-section plots was established in the treated areas, and losses on these plots were measured for the period 1946–50. Similar plots and loss studies were made in adjacent virgin stands where no control work was done. Results of these studies were summarized in reports by Bongberg (*U32*, *U33*). The pine losses under the three methods of control were as follows:

Method:	Area sampled (acres)	Loss before control, 1945 (bd. ft.)	Loss after control	
			1946 (bd. ft.)	1947 (bd. ft.)
Virgin areas (no control)	1, 826	65. 1	49. 1	62. 3
Fell-peel-burn (maintenance control)	2, 532	55. 9	66. 7	86. 5
Sanitation-salvage	1, 176	111. 0	27. 4	17. 4
Modified sanitation-salvage	676	82. 1	24. 0	6. 2

Direct control by the fell-peel-burn method, although it was applied over a large acreage, had little or no effect on this endemic infestation; subsequent losses even exceeded those in the virgin areas. On the other hand, indirect control through sanitation-salvage caused an immediate reduction in loss the first year and even greater reduction the second year. The additional benefits derived from the more intensive modified sanitation-salvage treatment are not considered to be large enough to warrant the additional costs of this method.

CONTROL POLICY

Questions of how, why, and under what conditions to apply control measures against the western pine beetle involve all that has been learned about this insect. Questions of control policy must take into consideration not only the entomological factors, but also time, place,

and economic factors. General policies to govern control recommendations are not easily defined. Nearly every control project has had its own special conditions affecting control policy.

Periodically, efforts have been made to set forth the more salient factors affecting the application of control practices. Craighead, Miller, Evenden, and Keen (*26*) summarized the experience on western pine beetle control projects up to 1930, and on this basis drew conclusions and recommendations for a control policy as follows:

> 1. The success of direct western pine beetle control has not been spectacular or outstanding but in many cases has shown tangible results.
> 2. One season of thorough work results in reduction of losses.
> 3. The benefits are greatest when the natural trend of infestation is upward.
> 4. The benefits of direct control are temporary and must be continued to maintain control. Under these conditions we recommended direct control after considering both economic and entomological factors. . . . .
>
> . . . In parks and on recreational areas where trees are of high value from the aesthetic standpoint.
>
> . . . On small well-isolated areas where the timber is of high value and where the entire infestation can be treated in one season.
>
> . . . On large areas, preferably with partial isolation, where the entire infested area can be treated and where it is to be logged within 3 or 4 years.
>
> . . . In commercial stands, whether isolated or not, where control work can be supplemented by logging and the treated trees salvaged at a low cost or a profit. Such work may be combined with selective logging to remove susceptible trees and produce better growth conditions in order to give permanent protection for long periods.

In 1935 the Branch of Forestry of the National Park Service (*135*) established an insect control policy to be followed on national-park areas. After a definition of the types of areas in which insect control would be considered, the following statement was made specifically for the western pine beetle:

> This beetle takes annually a small percentage of the stand and at intervals of some years a considerably larger percentage. The main objective in controlling the depredations of this beetle would be to prevent the peaks of this type of infestation and thus prolong the life of the existing stand over a longer rotation or gradual replacement; in other words, the objective would be to carry on a certain amount of maintenance control from year to year in an effort to keep the losses at the lowest possible status all the time.

Because of the outstanding success of sanitation-salvage in controlling western pine beetle epidemics, particularly in commercial stands, the policy regarding use of direct methods was greatly modified after 1942. Sanitation-salvage was recommended in all interior ponderosa pine types where the timber could be cut and utilized.

Direct control was then limited to a restricted number of situations where sanitation-salvage was not suitable.

Indirect control through sanitation-salvage is most appropriate in commercial pine areas where a precutting of the highest risk trees can be applied and the logs can be utilized. Transportation developments in the area, facilities for logging and milling, and available markets must be taken into account. These factors largely determine whether indirect control is feasible. The statement published by Keen and Salman (*82*) in 1942 outlines the general policy in the applicability of sanitation-salvage control:

> Beetle control through tree selection and sanitation logging offers many advantages over the previous fell-peel-burn method of direct control. Results of tests so far show a greater reduction in subsequent losses than is usually obtained by the older method. Moreover, the recovery of timber values which would otherwise be lost may offset much of the cost of treatment and may even yield a profit. On the other hand, this method is limited in its application to commercial timber stands of fairly high value that can be reached by logging operations at a reasonable cost. This method is not appropriate for beetle control in parks, recreational areas, or inaccessible commercial forest areas in rough terrain. For such situations as these, fell-peel-burn or other direct control methods still offer the only practicable measures that can be used.

On the basis of current knowledge, a new bark beetle control policy statement was outlined by Keen (*164*) in 1949:

Indirect Bark Beetle Control

In all western pine stands such silvicultural measures as thinnings and partial cuttings for improved forest sanitation, particularly the selective cutting of trees of poor thrift and the removal of high-risk trees, tend to leave a more vigorous residual stand of timber which should be more resistant to bark beetle attack. Therefore, such measures are endorsed as a part of sound timber management practices and for whatever benefit may be gained in minimizing bark beetle losses.

For the present, sanitation-salvage logging as a bark beetle control measure will be recommended only for the virgin commercial ponderosa and Jeffrey pine stands on the east slope of the Sierra Nevada and Cascade Mountains in California, Oregon, and Washington where the percentage of high-risk trees, as defined by Salman and Bongberg, in the stand exceeds 10 percent and where a light cutting is feasible from the economic standpoint—i.e., where the cost of the work can be largely offset by the value of logs salvaged. In high-hazard areas (Hazard V Zone) and on fringe areas where the high-risk element of the stand exceeds 40 percent of the volume, some system of heavy cutting to utilize merchantable timber will normally be recommended, rather than a sanitation-salvage cutting for beetle control purposes only.

In west-side stands of ponderosa, sugar, and Jeffrey pine and in all white pine and lodgepole pine stands, sanitation-salvage logging as a measure of bark-beetle control is not being recommended at the present time.

Direct Bark Beetle Control

This method of control may be recommended in situations where sanitation-salvage is not applicable and where the following conditions apply:

Western Pine Beetle Control

A. *Entomological conditions*

Strong broods of bark beetles in single trees or small groups, and infestations showing signs of increasing aggressiveness and an upward trend. Endemic infestations will not be treated except as maintenance control in highly valuable recreational areas or where cost can be largely offset by salvage. Epidemic infestations may be treated to hasten decline, but if advanced too far, may be considered as beyond practical control measures. The entomological considerations warranting control cannot be stated precisely but require the exercise of good judgment based upon technical factors and past experience.

B. *Area conditions*

(1) Park or recreational areas with or without complete isolation where trees are of high value from an aesthetic standpoint. Annual maintenance control is justified in such areas.

(2) Small areas, well isolated from other infested areas, where entire area can be treated in one season. Recleaning in the second season depends upon character and intensity of new infestation.

(3) Large areas, preferably with partial isolation, where the entire infested area can be treated, and which are to be logged or come under management within 3 or 4 years (before reinfestation develops). Recleaning in the second season depends upon character and intensity of new infestation.

(4) Commercial stands, whether isolated or not, where control work can be supplemented by logging and the infested timber can be salvaged at a low cost or a small profit. Wherever possible, such work should be combined with selective logging to remove susceptible trees and produce better growth conditions in order to give protection for longer periods.

C. *Economic conditions*

While the entomologist must take cognizance of economic considerations, the economic justification for control is a matter which must be decided primarily by the timber owner. In general, the cost of control work should not exceed the value of benefits to be derived. The benefits include: (a) actual timber values saved, and (b) intangible values such as protection of watershed cover and grazing, aesthetic values, and reduction of fire hazard. In parks and highly valuable recreational areas, costs may be high and still be justified by the aesthetic values involved. On commercial areas the cost of control if applied against an increasing infestation might be justified up to three to five times the stumpage value of the timber infested, while with decreasing infestations, the treating cost per thousand board feet probably should not exceed one-half the value of the stumpage.

FURTHER RESEARCH NEEDS

The completion of this review does not mean that we can write "finis" to investigations of the western pine beetle. In spite of the fact that this bark beetle has received more study than any other western forest insect, many phases of this research have been merely exploratory, and many answers are yet to be found.

The beetle's biology, seasonal history, and habits have been quite thoroughly covered and are essentially complete except for two phases: flight habits of the beetle have not been fully determined, nor has much progress been made in determining why the beetles are attracted to certain trees and not to others. Or is this merely a matter of host resistance and susceptibility? If a definitely attractive substance could be found, it would open up a new field of control in baiting and trapping.

Much work has been done to determine the biotic potential of the western pine beetle and the factors that cause brood mortality within the brood tree, but we have scant knowledge of what happens to the beetles after they leave the brood tree and before they make successful attacks on the next generation trees. Yet it appears that during the flight period the greatest mortality occurs, so much in some cases that no correlation can be found between the density of emerging populations and subsequent tree mortality. Tree mortality from year to year seems to be quite unrelated to the abundance of western pine beetle populations. Even a 90-percent kill of beetle broods by subzero weather over extensive forest areas had only a temporary effect on the trend of timber losses. Nor do large populations necessarily make for severe timber damage.

We still need to discover the reasons for epidemic timber damage and to learn how outbreaks can be predicted. Epidemics do not seem to be related to a buildup of beetle populations, nor do they appear to be directly related to climatic or host conditions.

Direct control measures aimed at killing beetle populations have been quite fully explored and applied over vast areas for many years. Some improvements might be made in the use of toxic chemicals to lower the cost of such work. However, all results from applied control indicate that the killing of beetles, no matter by what method, has only a limited effect in reducing tree mortality. The trend of epidemics is only temporarily altered by direct control.

The use of residual sprays to protect trees from attack has not been fully explored. The development of such preventive treatment would be particularly useful in the protection of valuable trees around summer homes and in recreational areas.

The development of resistant strains of pine has not been studied as yet. If such strains could be developed, future forests might be made beetle resistant.

Ecological and silvicultural relations have received study, but more research in these fields is needed, particularly in westside stands and on the better sites. Further study is needed to evaluate the importance of various factors associated with the western pine beetle

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in killing ponderosa pine. The role of flathead infestations in developing high-risk trees needs further study; also, the importance of such factors as root rots (particularly *Fomes annosus*), drought, competition, slow growth, and poor tree vigor need further study to determine the basic factors of tree susceptibility, resistance, and the relative role of different factors in bringing about ultimate tree mortality.

Reduction of timber losses through sanitation-salvage logging hits most directly at the basic causes of ponderosa pine mortality, and has proved outstandingly successful as a beetle control measure in eastside pine stands. So far the application of this method is limited to accessible eastside stands where the cost of this type of logging is not prohibitive. The possibility of adapting a similar silvicultural method to beetle control in westside stands needs further study of the basic ecological factors.

These are only a few of the more obvious unsolved problems that should give future research workers plenty of room for expanding knowledge of this important forest insect.

LITERATURE CITED

(1) Anonymous.
1945. salvage logging. Timberman 46(6): 98–100, illus.

(2) ———
1946. DDT shows promising results in beetle control. Timberman 48(2): 52, 54, 62, illus.

(3) Beal, J. A.
1934. relation of air and bark temperatures of infested ponderosa pines during sub-zero weather. Jour. Econ. Ent. 27: 1132–1139, illus.

(4) Bedard, W. D.
1938. control of the mountain pine beetle by means of chemicals. Jour. Forestry 36: 35–40, illus.

(5) Blackman, M. W.
1931. the black hills beetle (dendroctonus ponderosae hopk.) N.Y. State Col. Forestry, Syracuse Univ. Bul. 4(4), Tech. Pub. 36, 77 pp., illus.

(6) Bongberg, J. W.
1947. experimental cutting for beetle control. Timberman 48(7): 128–130, illus.

(7) Boyce, J. S.
1923. deterioration of felled western yellow pine on insect control projects. U.S. Dept. Agr. Bul. 1140, 7 pp., illus.

(8) Brandstrom, A. J. F.
1947. the role of selective cutting in promoting sustained yield with special reference to ponderosa pine. Jour. Forestry 35: 142–147.

(9) Briegleb, Philip A.
1940. forest growth in the ponderosa pine region of oregon and washington. U.S. Forest Serv. Pacific Northwest Forest and Range Expt. Sta. Forest Survey Rpt. 78. [Processed.]

(10 ———
1943. growth of ponderosa pine by keen tree class. U.S. Forest Serv. Pacific Northwest Forest Expt. Sta. Res. Note 32, 15 pp., illus. [Processed.]

(11) ———
1945. calculating the growth of ponderosa pine forests. U.S. Dept. Agr. Forest Service, Portland, Oreg. Dec. 28, 1945, illus. [Processed.]

(12) Brundage, M. R., and Orr, T. J.
1936. lumber selling values from insect-infested ponderosa and jeffrey pine trees salvaged in 1935 on an eastside pine region area. U.S. Forest Serv. Calif. Forest and Range Expt. Sta. Res. Note 9. April 10, 1936. [Processed.]

(13) Buckhorn, W. J.
1944. instructions for making bark beetle surveys in virgin pine stands of oregon and washington. U.S. Dept. Agr. Bur. Ent. and Plant Quar. Forest Insect Lab., Portland, Oreg. 64 pp. [Processed.]

(14) Burke, H. E.
1919. biological notes on some flatheaded bark borers of the genus melanophila. Jour. Econ. Ent. 12: 105–108.

(15) ———
1946. my recollections of the first years in forest entomology. Berkeley, Calif. June 28, 1946. 37 pp., illus. [Processed.]

(16) Caird, R. W.
1934. physiology of pines infested with bark beetles. Bot. Gaz. 96: 709–733.

(17) Chamberlin, W. J.
1920. the western pine beetle—a serious pest of western yellow pine in oregon. Oreg. Agr. Expt. Sta. Bul. 172, 33 pp., illus.

(18) Chamberlin, W. J.
1920. fighting pine beetles with electricity. Timberman 21(10): 38, illus.
(19) ———
1939. the bark and timber beetles of north america. Oreg. State Col. Coop. Assoc. Corvallis, Oreg. 513 pp., illus.
(20) Craighead, F. C.
1924. problems and methods in forest entomology. Jour. Forestry 22: 79–81.
(21) ———
1925. the dendroctonus problems. Jour. Forestry 23: 340–354.
(22) ———
1925. bark beetle epidemics and rainfall deficiency. Jour. Econ. Ent. 18: 577–586.
(23) ———
1927. the relation of insects to slash disposal. U.S. Dept. Agr. Cir 411, 12 pp.
(24) ———
1928. interrelation of tree-killing bark beetles (dendroctonus) and bluestain. Jour. Forestry 26: 886–887.
(25) ———
1942. the influence of insects on the development of forest protection and forest management. Smithsn. Inst. Rpt. 1941, Pub. 3665: 367–392, illus.
(26) ——— Miller, J. M., Evenden, J. C., and Keen, F. P.
1931. control work against bark beetles in western forests and an appraisal of its results. Jour. Forestry 29: 1001–1018.
(27) ——— and St. George, R. A.
1938. experimental work with the introduction of chemicals into the sap stream of trees for the control of insects. Jour. Forestry 36: 26–34.
(28) DeLeon, Donald.
1942. the red turpentine beetle, a pest of conifers in the california region. U.S. Bur. Ent. and Plant Quar. E–568, 4 pp., illus.
(29) Doane, R. W.
1927. the genus ips on the stanford campus. Jour. Econ. Ent. 20. 284–286.
(30) ——— Van Dyke, E. C., Chamberlin, W. J., and Burke, H. E.
1936. forest insects. 463 pp., illus. New York and London.
(31) Dunning, Duncan.
1928. a tree classification for the selection forests of the sierra nevada. Jour. Agr. Res. 36: 755–771, illus.
(32) Evenden, J. C.
1940. effects of defoliation by the pine butterfly. (neophasia menapia felder) upon ponderosa pine. Jour. Forestry 38: 949–955, illus.
(33) ———
1926. logging to check pine beetle. Timberman 27(4): 178–180, illus.
(34) ——— Bedard, W. D., and Struble, G. R.
1943. the mountain pine beetle, an important enemy of western pines. U.S. Dept. Agr. Cir. 664, 25 pp., illus.
(35) Gay, Norman.
1932. pine beetle problems. Res. and Devlpmt. Standard Oil Lab. Richmond, Calif. [Processed.]
(36) Gordon, A.
1938. studies on susceptibility of shade trees to destructive agencies. West. Shade Tree Conf. Proc. 5: 69–74.
(37) Graves, Henry S.
1920. the torch in the timber. Sunset 44(4): 37–40, 80–82, 86, 88, 90, illus.
(38) Hall, Elmer.
1944. thirty years' experience with bug control. West. Forestry and Conserv. Assoc. Proc. 35: 25–26.
(39) Hawley, Ralph C.
1944. forestry terminology. Soc. Amer. Foresters, Washington, D.C. 84 pp.

(40) Holst, E. C.
1936. zygosaccharomyces pini, a new species of yeast associated with bark beetles in pines. Jour. Agr. Res. 53: 513–518, illus.
(41) Hopkins, A. D.
1893. destructive scolytids and their imported enemy. Insect Life 6(2): 123–129.
(42) ———
1899. preliminary report on insect enemies of forests in the northwest. U.S. Dept. Agr. Bul. 21, 27 pp.
(43) ———
1909. the genus dendroctonus U.S. Dept. Agr. Tech. Ser. 17, Pt. I, 164 pp., illus.
(44) ———
1909. bark beetles of the genus dendroctonus. U.S. Dept. Agr. Bul. 83, Pt. I, 169 pp., illus.
(45) ———
1919. the bioclimatic law as applied to entomological research and farm practice. Sci. Monthly 8: 496–513, illus.
(46) ———
1920. the bioclimatic law. Wash. Acad. Sci. Jour. 10: 34–40.
(47) ———
1938. bioclimatics. U.S. Dept. Agr. Misc. Pub. 280, 188 pp., illus.
(48) Hopping, George R.
1937. insect injury to british columbia forests during the past decade. *In* Mulholland, F. D., the resources of british columbia. Brit. Columbia Dept. Lands, Forest Serv., pp. 62–63, illus.
(49) Hopping, Ralph.
1914. manual of insect control for california, district 5. U.S. Forest Serv., San Francisco, Calif. 66 pp. + 15-p. suppl. [Processed.]
(50) ———
1915. the entomological aspects of slash disposal. Soc. Amer. Foresters Proc. 10: 183–185.
(51) ———
1924. yellow pine (pinus ponderosa) as a host in british columbia. Canad. Ent. 56: 125–128.
(52) ———
1925. relation between abnormality and insect attack in western yellow and jeffrey pine stands. Jour. Forestry 23: 932–935.
(53) ———
1928. influence of slash on bark beetle outbreaks. Forestry Chron. 4(2). [n.p.] June.
(54) Johnson, P. C.
1935. field manual of bark beetle survey methods, california region. U.S. Bur. Ent. and Plant Quar. Forest Insect Lab., Berkeley, Calif. May 1, 1935. Rev. May 1, 1936. 34 pp. [Processed.]
(55) ———
1940. entomological considerations in the utilization of insect-killed ponderosa pine. Jour. Econ. Ent. 33: 773–776.
(56) ———
1949. determining the bark-beetle hazard of pine stands in northeastern california. Jour. Forestry 47: 277–284, illus.
(57) ———
1951. application of risk ratings for western pine beetle control in the inland empire. Northwest Sci. 25: 32–37.
(58) Keen, F. P.
1923. war on the pine beetle. Amer. Forestry 29 (359): 689–694, illus.
(59) ———
1926. administration of western pine beetle control projects. U.S. Bur. Ent. and Plant Quar. Stanford Univ., Calif. [Processed.]
(60) ———
1926. pine beetle control in southern oregon and northern california. Timberman 27(5): 178–182.

(61) KEEN, F. P.
1927. MANUAL OF BARK BEETLE CONTROL IN WESTERN PINE FORESTS. U.S. Forest Serv. Region 5, 58 pp. [Processed.]
(62) ———
1928. INSECT ENEMIES OF CALIFORNIA PINES AND THEIR CONTROL. Calif. Dept. Nat. Resources, Div. Forestry Bul. 7, 113 pp., illus.
(63) ———
1929. LODGEPOLE NOT TABOO TO WESTERN PINE BEETLE. U.S. Forest Serv. Forest Worker 5(2): 18.
(64) ———
1929. WESTERN PINE BEETLE ATTACKS NEW HOST. Pan-Pacific Ent. 5: 108.
(65) ———
1929. HOW SOON DO YELLOW PINE SNAGS FALL. Jour. Forestry 27: 735–737, illus.
(66) ———
1931. PINE BEETLE CONTROL COSTS REDUCED THROUGH LOGGING AND SALVAGE. U.S. Dept. Agr. Yearbook 1931: 428–430, illus.
(67) ———
1933. A NOTE ON THE HIBERNATION HABITS OF SOME ENGRAVER BEETLES OF THE GENUS IPS. Jour. Econ. Ent. 26: 297–298.
(68) ———
1936. RELATIVE SUSCEPTIBILITY OF PONDEROSA PINE TO BARK BEETLE ATTACK. Jour. Forestry 34: 919–927, illus.
(69) ———
1937. CLIMATIC CYCLES IN EASTERN OREGON AS INDICATED BY TREE RINGS. U.S. Monthly Weather Rev. 65(5): 175–188, illus.
(70) ———
1940. LONGEVITY OF PONDEROSA PINE. Jour. Forestry 38: 597–598.
(71) ———
1943. PONDEROSA PINE TREE CLASSES REDEFINED. Jour. Forestry 41: 249–253, illus.
(72) ———
1946. ENTOMOLOGY IN WESTERN PINE SILVICULTURE. Pan-Pacific Ent. 22: 1–8.
(73) ———
1946. A TREE-CLASS SLIDE RULE. Jour. Forestry 44: 755–757, illus.
(74) ———
1950. THE INFLUENCE OF INSECTS ON PONDEROSA PINE SILVICULTURE. Jour. Forestry 48: 186–188.
(75) ———
1952. INSECT ENEMIES OF WESTERN FORESTS. U.S. Dept. Agr. Misc. Pub. 273, 280 pp., illus. Rev. ed.
(76) ———
1952. BARK BEETLES IN FORESTS. U.S. Dept. Agr. Yearbook 1952: 688–694.
(77) ———
1955. THE WESTERN PINE BEETLE. U.S. Dept. Agr. Forest Pest Leaflet 1, 4 pp., illus.
(78) ———
1955. THE RATE OF NATURAL FALLING OF BEETLE-KILLED PONDEROSA PINE SNAGS. Jour. Forestry 53: 720–723, illus.
(79) ———
1956. LOW TEMPERATURE DIFFERENTIALS IN ONE FOREST DRAINAGE. Ecology 37: 381–383, illus.
(80) ———
1958. PROGRESS IN BARK BEETLE CONTROL THROUGH SILVICULTURE IN THE UNITED STATES. Tenth Internatl. Cong. Ent. Proc. 4: 171–180.
(81) ——— AND FURNISS, R. L.
1937. EFFECTS OF SUB-ZERO TEMPERATURES ON POPULATIONS OF WESTERN PINE BEETLE. Jour. Econ. Ent. 30: 482–504, illus.
(82) ——— AND SALMAN, K. A.
1942. PROGRESS IN PINE BEETLE CONTROL THROUGH TREE SELECTION. Jour. Forestry 40: 854–858.
(83) LECONTE, J. L.
1876. RHYNCOPHORA OF AMERICA NORTH OF MEXICO. Amer. Phil. Soc. Proc. 15(96): 455 pp.

(84) Lightle, P. C.
1954. the pathology of elytroderma deformans on ponderosa pine. Phytopathology 44: 557–569, illus.
(85) Linsley, E. Gorton.
1943. attraction of melanophila beetles by fire and smoke. Jour. Econ. Ent. 36: 341–342, illus.
(86) Martin, C. S.
1937. pine beetle logging company. Amer. Forests 43: 122, 144, illus.
(87) McDaniels, E. H.
1940. beating the beetles. Amer. Forests 46: 506–508, illus.
(88) McKenzie, H. L.
1941. matsucoccus bisetosus morrison, a potential enemy of california pines. Jour. Econ. Ent. 34: 783–785, illus.
(89) Miller, J. M.
1912. how the insect control problem compares with the fire problem on national forests in district five. Forestry Quart. 10(2): 208–214.
(90) ———
1921. fighting western pine beetles. Timberman 23(1): 40–41, illus.
(91) ———
1925. methods of estimating bark beetle losses. Timberman 26(8): 186–188, illus.
(92) ———
1926. the western pine beetle control problem. Jour. Forestry 24: 897–910.
(93) ———
1928. the relation of windfalls to bark beetle epidemics. Fourth Internatl. Cong. of Ent. Trans. 2: 992–1002, illus.
(94) ———
1930. extremes of temperature fatal to western pine beetle. U.S. Forest Serv. Forest Worker 6(1): 17.
(95) ———
1931. high and low lethal temperatures for the western pine beetle. Jour. Agr. Res. 43: 303–321, illus.
(96) ———
1933. a record of winter kill of western pine beetle in california. Jour. Forestry 31: 443–446.
(97) ———
1933. mortality of the western pine beetle due to low temperatures on the badger springs insect control project, modoc national forest, during december 1932. U.S. Bur. Ent. and Plant Quar. Forest Insect Lab., Berkeley, Calif. Jan. 19, 1933. 5 pp. [Processed.]
(98) ———
1933. effects of low temperatures during the winter of 1932–33 upon pine beetle populations in california. U.S. Bur. Ent. and Plant Quar. Forest Insect Lab., Berkeley, Calif. April 10, 1934, 5 pp., illus. [Processed.]
(99) ——— and Patterson, J. E.
1927. preliminary studies on the relation of fire injury to bark beetle attack in western yellow pine. Jour. Agr. Res. 34: 597–613, illus.
(100) ——— Salman, K. A., and Johnson, P. C.
1941. bark beetle hazards in the pine stands of northeastern california. U.S. Bur. Ent. and Plant Quar. Forest Insect Lab., Berkeley, Calif. May 15, 1941. Pt. I, 15 pp., illus; Pt. II, 277 pp., illus. [Processed.]
(101) Nelson, R. M., and Beal, J. A.
1929. experiments with bluestain fungi in southern pines. Jour. Amer. Phytopath. Soc. 19: 1101–1106.
(102) Olson, A. J.
1941. a root disease of jeffrey and ponderosa pine reproduction. Phytopathology 31: 1063–1077.
(103) Orr, Thomas J.
1942. reducing pine beetle damage through partial cutting. West Coast Lumberman 69(4): 42–46, 79, illus., April.

(104) Orr, Thomas J.
1945. selective marking in ponderosa pine on a klamath falls tree farm. Jour. Forestry 43: 738–741, illus.
(105) Patterson, J. E.
1923. pine beetle control in northern california. Timberman 24(8): 38, illus.
(106) ———
1927. the relation of highway slash to infestations of the western pine beetle. U.S. Dept. Agr. Tech. Bul. 3, 9 pp., illus.
(107) ———
1929. the pandora moth, a periodic pest of western pine forests. U.S. Dept. Agr. Tech. Bul. 137, 19 pp., illus.
(108) ———
1930. milling beetle-killed pine timber. Timberman 31(3): 162–172, illus.
(109) ———
1930. control of the mountain pine beetle in lodgepole pine by the use of solar heat. U.S. Dept. Agr. Tech. Bul. 195, 19 pp., illus.
(110) ———
1935. forest insect problems of the yosemite national park. U.S. Bur. Ent. and Plant Quar., Div. Forest Insect Inv., and Field Div. Forestry, Natl. Park Serv., Berkeley, Calif. Dec. 1, 1935. 25 pp. [Processed.]
(111) Person, H. L.
1928. tree selection by the western pine beetle. Jour. Forestry 26: 564–578, illus.
(112) ———
1931. theory in explanation of the selection of certain trees by the western pine beetle. Jour. Forestry 29: 696–699.
(113) ———
1940. the clerid thanasimus lecontei wolc., as a factor in the control of the western pine beetle. Jour. Forestry 38: 390–396, illus.
(114) Robinson, W.
1928. determination of the natural undercooling and freezing points in insects. Jour. Agr. Res. 37: 749–755.
(115) Rumbold, Caroline T.
1931. two bluestaining fungi associated with bark beetle infestation of pines. Jour. Agr. Res. 43: 847–873, illus.
(116) ———
1941. a bluestain fungus, ceratostomella montium n. sp., and some yeasts associated with two species of dendroctonus Jour. Agr. Res. 62: 589–601, illus.
(117) Rust, H. J.
1933. many bark beetles destroyed by predaceous mites. Jour. Econ. Ent. 26: 733–734.
(118) Salman, K. A.
1934. entomological factors affecting salvaging of fire-injured trees. Jour. Forestry 32: 1016–1017.
(119) ———
1938. recent experiments with penetrating oil sprays for the control of bark beetles. Jour. Econ. Ent. 31: 119–123.
(120) ———
1938. an unusual type of topkill of ponderosa pine. Jour. Econ. Ent. 31: 613–616, illus.
(121) ——— and Bongberg, J. W.
1942. logging high risk trees to control insects in pine stands of northeastern california. Jour. Forestry 40: 533–539.
(122) Sowder, J. E.
1951. a sanitation-salvage cutting in ponderosa pine, pringle falls experimental forest. U.S. Forest Serv. Pacific Northwest Forest and Range Expt. Sta. Res. Paper 2, 24 pp., illus. [Processed.]

(123) Steiner, G.
1932. some nemic parasites and associates of the mountain pine beetle (dendroctonus monticolae). Jour. Agr. Res. 45: 437–444, illus.
(124) Steinhaus, E. A.
1949. principles of insect pathology. 757 pp., illus. New York, Toronto, London.
(125) Struble, G. R.
1930. the biology of certain coleoptera associated with bark beetles in western yellow pine. Calif. Univ. Pubs., Ent. 5(6): 105–134, illus.
(126) ———
1942. biology of two native predators of the mountain pine beetle in sugar pine. Pan-Pacific Ent. 18: 97–107, illus.
(127) ———
1942. laboratory propagation of two predators of the mountain pine beetle. Jour. Econ. Ent. 35: 841–844, illus.
(128) ———
1948. pine blowdown causes outbreak of western pine beetle. Jour. Forestry 46: 129–130.
(129) ——— and Hall, R. C.
1955. the california five-spined engraver, its biology and control. U.S. Dept. Agr. Cir. 964, 21 pp., illus.
(130) Stump, E. L.
1936. trees on state highway saved from destruction by western pine beetle. Calif. Highways and Pub. Works Jour., April, pp. 10, 26, 32, illus.
(131) Swaine, J. M.
1914. forest insect conditions in british columbia. Canada Expt. Farms, Div. Ent. Bul. 7, 41 pp., illus.
(132) ———
1918. canadian bark beetles, part ii: a preliminary classification with an account of the habits and means of control. Canada Dept. Agr. Bul. 14, 143 pp., illus.
(133) Thorne, Gerald.
1935. nemic parasites and associates of the mountain pine beetle (dendroctonus monticolae) in utah. Jour. Agr. Res. 51: 131–144, illus.
(134) U.S. Forest Service, Region Six.
1933. forest insect handbook, north pacific region. Portland, Oreg., April 1933. 115 pp., illus. [Processed.]
(135) U.S. National Park Service.
1938. manual of the branch of forestry. 76 pp.
(136) Wagener, Willis W.
1949. top dying of conifers from sudden cold. Jour. Forestry 47: 49–53.
(137) ——— and Cave, Marion S.
1946. pine killing by the root fungus, fomes annosus, in california. Jour. Forestry 44: 47–54, illus.
(138) ——— and Davidson, Ross W.
1954. heart rots in living trees. Bot. Rev. 20(2): 61–134.
(139) Walther, E.
1933. a practical method of controlling dendroctonus valens lec. Jour. Econ. Ent. 26: 828–831, illus.
(140) Wear, J. F., and Bongberg, J. W.
1951. uses of aerial photographs in control of forest insects. Jour. Forestry 49: 632–633.
(141) Weaver, Harold.
1934. the development and control of pine beetle epidemics. Jour. Forestry 32: 100–103.
(142) ———
1943. fire as an ecological and silvicultural factor in the ponderosa pine region of the pacific slope. Jour. Forestry 41: 7–15, illus.

(143) Weaver, Harold.
1955. fire as an enemy, friend, and tool in forest management. Jour. Forestry 53: 499–504, illus.
(144) Webb, J. L.
1906. the western pine destroying bark beetle. U.S. Dept. Agr. Bur. Ent. Bul. 58, Pt. II, 30 pp., illus.
(145) Weir, James R.
1916. mistletoes injury to conifers in the northwest. U.S. Dept. Agr. Bul. 360, 39 pp., illus.
(146) West, A. S., Jr.
1947. the california flatheaded borer (melanophila californica van dyke) in ponderosa pine stands of northeastern california. Canad. Jour. Res. 25, Sect. D, Zool. Sci., pp. 97–118, illus.
(147) White, Stewart Edward.
1916. tree killing barkbeetles of california and possible remedies. Amer. Lumberman 2169: 30, 31, Dec. 9, 1916.
(148) ———
1917. surface burning. Amer. Lumberman 2182: 36–37, March 10, 1917.
(149) ———
1920. woodsmen, spare those trees. Sunset 44(3): 23–26, 108, 110, 112, 114, 115, 116, illus.
(150) Whiteside, J. M.
1951. the western pine beetle. U.S. Dept. Agr. Cir. 864, 11 pp., illus.
(151) Yuill, J. S.
1941. cold hardiness of two species of bark beetles in california forests. Jour. Econ. Ent. 34: 702–709, illus.

UNPUBLISHED MANUSCRIPT REPORTS [9]

(U1) Baumhofer, L. F.
1935. Memorandum on the *Ips* situation in the Harney and Black Hills National Forests. Fort Collins, Colo. (May 1935.)

(U2) ——— and Hauke, Harold A.
1936. Observations and preliminary studies on *Ips oregoni* in the Black Hills thinning areas. Fort Collins, Colo. (Apr. 20, 1936.)

(U3) Beal, J. A.
1930. Phloem moisture and beetle susceptibility of western yellow pine. Portland, Oreg. (Jan. 2, 1930.)

(U4) ———
1930. Insect increase in logging operations in western yellow pine. Portland, Oreg. (Jan. 15, 1930.)

(U5) ———
1930. The effect of a large logging operation on beetle populations. Prog. rpt. Portland, Oreg. (Dec. 1930.)

(U6) ———
1931. Relation of temperature and moisture to brood development of the western pine beetle. Portland, Oreg. (May 1931.)

(U7) Beal, J. A.
1931. Further studies of insects in logging operations in western yellow pine. Prog. rpt. Portland, Oreg. (Jan. 1931.)

(U8) ———
1932. Logging and the western pine beetle. Final rpt. Portland, Oreg. (Jan. 1932.)

(U9) ———
1932. The effect of ponderosa pine slash on insect abundance. Final rpt. Portland Oreg. (Feb. 1932.)

(U10) ———
1933. Relation of air and bark temperatures of infested ponderosa pines during subzero weather. Portland, Oreg. (Feb. 24, 1933.)

(U11) ———
1934. Western pine beetle emergence as affected by low winter temperatures. Portland, Oreg. (Feb. 1934.)

(U12) Bedard, W. D.
1941. Results of preliminary studies concerning the condition of beetle-susceptible ponderosa pines. Portland Oreg. (Mar. 24, 1941.)

(U13) ———
1942. Root studies I: preliminary attempts to study the root systems of mature ponderosa pines. Portland, Oreg. (Feb. 23, 1942.)

(U14) ———
1942. Root studies II: experimental plan to test the effects of soil moisture, certain soil nutrients, and physical injuries on ponderosa pine development. Portland, Oreg. (Feb. 23, 1942.)

(U15) ———
1942. The relative annual growth of different ponderosa pine meristems and its importance in evaluating current health symptoms. Portland, Oreg. (Mar. 18, 1942.)

[9] Copies of the reports listed here, are on file at the Pacific Southwest Forest and Range Experiment Station, Berkeley, Calif., and copies of most of them are at the Pacific Northwest Forest and Range Experiment Station, Portland, Oreg. Anyone interested may consult the files, but copies of the reports are not available for distribution or loan.

(U16) Bedard, W. D.
1942. Effect of irrigation on radial growth in large ponderosa pine trees. Portland, Oreg. (Mar. 19, 1942.)
(U17) ———
1943. An analysis of factors associated with insect loss on one-acre plots in eastern Oregon and Washington. Portland, Oreg. (Apr. 24, 1943.)
(U18) ———
1944. Third year's results of the pine beetle control logging tests of the Weyerhaeuser Timber Company, Rail Glade area, Bly district, Oreg. Berkeley, Calif. (Feb. 12, 1944.)
(U19) ———
1944. Results of pine beetle control logging by the Weyerhaeuser Timber Company on the Swede Cabin area, Bly district, Oreg. Berkeley, Calif. (Feb. 17, 1944.)
(U20) ———
1944. Mortality rate of risk marked ponderosa pine on the uncut check areas in the Bly district, Oregon. Prog. rpt. of first 3 years' results. Berkeley, Calif. (May 3, 1944.)
(U21) ———
1944. The effect of certain soil and injury treatments on the growth of ponderosa pine. Berkeley, Calif. (Oct. 2, 1944.)
(U22) Bongberg, J. W.
1938. Tree susceptibility studies on Blacks Mountain Experimental Forest. Prog. rpt. Berkeley, Calif. (Feb. 26, 1938.)
(U23) ———
1939. Loss prevention studies, Blacks Mountain Experimental Forest, season of 1938. Berkeley, Calif. (May 12, 1939.)
(U24) ———
1941. Effect of red turpentine beetle on cutover areas in providing green trees more susceptible to primary bark beetles. Berkeley, Calif. (Feb. 17, 1941.)
(U25) ———
1941. Effectiveness of sanitation-salvage logging in reducing insect-caused loss, Blacks Mountain Experimental Forest, season of 1940. Berkeley, Calif. (May 12, 1941.)
(U26) ———
1942. Pine beetle control through sanitation-salvage, Dixie Valley sale area, Plumas National Forest, Calif. Berkeley, Calif. (Dec. 14, 1942.)
(U27) ———
1942. The reliability of crown characters for appraisals of risk to ponderosa pines. Berkeley, Calif. (Mar. 26, 1942.)
(U28) ———
1943. Selective logging for the prevention of timber loss caused by insects, Hog Lake compartment, Happy Camp-Lava Beds area, Modoc National Forest. Berkeley, Calif. (Jan. 1, 1943.)
(U29) ———
1943. Effectiveness of light salvage cuttings at Cayton and Harris Mountain in reducing beetle-caused loss. Berkeley, Calif. (Dec. 13, 1943.)
(U30) ———
1944. A preliminary analysis of risk ratings used in appraising bark beetle susceptibility of ponderosa and Jeffrey pines. Berkeley, Calif. (Feb. 16, 1944.)
(U31) ———
1946. Fourth and fifth years' results of the pine beetle control logging test of the Weyerhaeuser Timber Company, Rail Glade area, Bly district, Oreg. Berkeley, Calif. (May 6, 1946.)
(U32) ———
1947. A comparison of results obtained by direct and indirect methods of bark beetle control in the Burney area, Shasta County, Calif. Berkeley, Calif. (Apr. 4, 1947.)
(U33) ———
1948. A comparison of benefits obtained by direct and indirect methods of bark beetle control in the Burney area, Shasta County, Calif. Berkeley, Calif. (Dec. 15, 1948.)

(U34) Bongberg, J. W.
1949. Results of ten years of bark beetle control by logging high risk trees, Blacks Mountain Experimental Forest, Lassen County, Calif. Berkeley, Calif. (May 6, 1949.)
(U35) ———
1949. Final results of pine beetle control logging test of Weyerhaeuser Timber Company, Rail Glade area, Bly district, Oreg. Berkeley, Calif. (June 2, 1949.)
(U36) ———
1949. Seven years' results of pine beetle control logging by Weyerhaeuser Timber Company, Swede Cabin area, Bly district, Oreg. Berkeley, Calif. (June 7, 1949.)
(U37) Buckhorn, W. J.
1934. Caging studies in central Oregon with western pine beetle and associated insects, season of 1933. Prog. rpt. Portland, Oreg. (Apr. 15, 1934.)
(U38) ———
1935. Caging studies in central Oregon with western pine beetle and associated insects. Prog. rpt. Portland, Oreg. (May 1, 1935.)
(U39) ———
1936. Caging studies in central Oregon with western pine beetle and associated insects. Prog. rpt. Portland, Oreg. (Feb. 21, 1936.)
(U40) ———
1943. Preliminary report on the relation of logging operations to outbreaks of *Ips oregoni* in ponderosa pine forests. Portland, Oreg. (July 8, 1943.)
(U41) ——— and Furniss, R. L.
1937. Report for period January 8–15; re: low temperatures, Ochoco National Forest. Portland, Oreg. (Jan. 16, 1937.)
(U42) Burke, H. E.
1912. Craggy, Barkhouse, and Moffatt Creek insect control projects. Yreka, Calif. (June 14, 1912.)
(U43) ———
1912. Report to Dr. A. D. Hopkins on the Antelope Creek project. Placerville, Calif. (Dec. 2, 1912.)
(U44) Caird, R. W.
1931. Physiology of trees attacked by bark beetles and their associated fungi. Sta. rpt. Asheville, N.C.
(U45) Callaham, R. Z.
1951. An investigation of Jeffrey pine mortality in the laguna recreation area. Berkeley, Calif. (Mar. 27, 1951.)
(U46) ———
1952. Negative phototropism of the Jeffrey pine beetle *Dendroctonus jeffreyi*. Memo. for the files. Berkeley, Calif. (Jan. 31, 1952.)
(U47) ———
1952. Studies of the olfactory and air current tropisms of the western pine beetle. Prog. rpt. season of 1951. Berkeley, Calif. (Apr. 1, 1952.)
(U48) ———
1952. The role of quantitative oleoresin production in the susceptibility of pines to bark beetles. Berkeley, Calif. (Apr. 14, 1952.)
(U49) ———
1952. Host selection and host susceptibility in the western pine beetle–ponderosa pine complex. Berkeley, Calif. (July 17, 1952.)
(U50) ———
1953. Studies of the resistance of pines to bark beetle attacks—season of 1952. Berkeley, Calif. (June 10, 1953.)
(U51) ——— and Miller, John M.
1952. Studies of the resistance of pine hybrids to bark beetle attacks—season of 1951. Berkeley, Calif. (Nov. 20, 1952.)
(U52) DeLeon, Donald.
1934. Report on 1933 losses of sugar pine and ponderosa pine in Sequoia National Park. Berkeley, Calif. (July 2, 1934.)
(U53) Durbrow, Houghton.
1930. A preliminary study of the hydrogen ion concentration in western yellow pine in relation to bark beetle attack. Berkeley, Calif. (Oct. 27, 1930.)

(U54) Eaton, Charles B.
1941. A photographic study of risk trees. Berkeley Calif. (June 25, 1941.)
(U55) ———
1942. Variation in the application of tree classification systems to ponderosa pine. Berkeley, Calif. (Mar. 11, 1942.)
(U56) ———
1942. The adaptation of aerial methods to the forest loss survey. Berkeley Calif. (Dec. 7, 1942.)
(U57) Engen, E. T.
1949. Forest insect survey of the Julian-Cuyamaca insect zone, season of 1948. Berkeley, Calif. (Feb. 9, 1949.)
(U58) ———
1949. The Julian-Cuyamaca bark beetle outbreak. Preliminary report of investigative studies. Berkeley, Calif. (May 27, 1949.)
(U59) Evenden, J. C.
1917. Seasonal history studies of *Dendroctonus brevicomis* in Idaho, 1916. Coeur d'Alene, Idaho. (Feb. 12, 1917.)
(U60) ———
1943. Summary report of low temperature studies, 1936–42. Coeur d'Alene, Idaho. (Feb. 18, 1943.)
(U61) Furniss, M. M.
1953. Inventory of current bark beetle hazard in yellow pine stands of the eastern Lassen area, Lassen National Forest, Calif. Berkeley, Calif. (May 8, 1953.)
(U62) ———
1954. A photographic study of the changes of insect risk in ponderosa pine. Berkeley, Calif. (May 14, 1954.)
(U63) Furniss, R. L.
1931. Line slash studies in western yellow pine, Hackamore, Calif. Berkeley Calif. (Jan. 1931.)
(U64) ———
1933. Biological considerations of *Dendroctonus brevicomis* in the North Fork region of California, 1932–33. Berkeley, Calif. (May 15, 1933.)
(U65) ———
1933. Studies of *Ips confusus*, North Fork, Calif., 1932. Berkeley, Calif. (May 15, 1933.)
(U66) ———
1934. Additional observations of the 1932–33 mortality of forest insects due to freezing, northeastern California. Berkeley, Calif. (Jan. 24, 1934.)
(U67) ———
1934. Preliminary observations of *Acanthocinus spectabilis* Lec. Berkeley, Calif. (Mar. 6, 1934.)
(U68) ———
1934. Seasonal history studies of *Dendroctonus brevicomis* in two areas in California. Berkeley Calif. (Apr. 1, 1934.)
(U69) ———
1936. Additional observations of the effects of low temperature upon overwintering populations of *Dendroctonus brevicomis*, Oregon, 1935. Portland, Oreg. (Feb. 19, 1936.)
(U70) Gibson, Archie L.
1936. Spraying with lethal oil to control the mountain pine beetle in lodgepole pine. Coeur d'Alene, Idaho. (Dec. 3, 1936.)
(U71) ———
1940. Screening lodgepole pine to prevent mountain pine beetle attack. Coeur d'Alene, Idaho. (Mar. 14, 1940.)
(U72) Glendenning, W. E.
1919. Bark examination, Rogue River area. Ashland, Oreg. (June 7, 1919.)
(U73) Gordon, Aaron.
1932. Tree injection in white fir and ecological studies of insects attacking ponderosa pine. Berkeley, Calif. (May 17, 1932.)
(U74) ———
1933. Apparatus used in a study of the western pine beetle. Berkeley, Calif. (June 21, 1933.)

(U75) Grant, R. C.
1941. The construction of a curve for predicting total annual loss from partial loss data in western pine beetle surveys. Portland, Oreg. (Apr. 21, 1941.)
(U76) Gustafson, Carl A.
1932. Insect control report, Sierra National Forest, Chiquito, Rock Creek, and Cascadel areas. North Fork, Calif. (July 15, 1932.)
(U77) ———
1933. Insect control report, Sierra National Forest, Fence Meadow, and Sugar pine sale projects. North Fork, Calif. (July 5, 1933.)
(U78) Hall, R. C.
1939. Forest insect surveys, Modoc National Forest, California. Season of 1938. Berkeley, Calif. (Feb. 8, 1939.)
(U79) ———
1939. Possible use of factors of bark and needle retention in dating snags. Berkeley, Calif. (Feb. 15, 1939.)
(U80) ———
1939. Some impressions of cyclical fluctuations of insect-caused losses in northeastern California. Berkeley, Calif. (Sept. 15, 1939).
(U81) ———
1940. A study of climatic influences on timber losses caused by insects in the ponderosa pine type of northern California for the season of 1939. Prog. rpt. Berkeley, Calif. (Mar. 14, 1940.)
(U82) ———
1941. Precipitation and insect loss in northeastern California. Memo. for Dr. Craighead. Berkeley, Calif. (Apr. 1, 1941.)
(U83) ———
1941. Some physiological factors associated with decadence in ponderosa pine. Berkeley, Calif. (May 16, 1941.)
(U84) ———
1942. Sampling methods in forest insect loss surveys in northeastern California. Berkeley, Calif. (Feb. 20, 1942.)
(U85) ———
1946. Accomplishments on the Burney-McCloud insect control project during 1945. Berkeley, Calif. (Feb. 25, 1946.)
(U86) ———
1946. DDT spray experiments for the control of the western pine beetle, season of 1945. Berkeley, Calif. (Aug. 5, 1946.)
(U87) ———
1947. Studies of *Ips* in northeastern California, season of 1946. Berkeley, Calif. (Apr. 16, 1947.)
(U88) ———
1949. An ecological study of *Ips confusus* in northern California. Prog. rpt. seasons of 1947 and 1948. Berkeley, Calif. (May 3, 1949.)
(U89) ———
1949. Climatic factors associated with *Ips* behavior. Berkeley, Calif. (June 20, 1949.)
(U90) ———
1953. An improved appraisal survey method for bark beetle damage in ponderosa and Jeffrey pine in the California region. Berkeley, Calif. (Feb. 6, 1953.)
(U91) ——— Terrell, T. T., Merkel, E. P., and others.
1951. Sampling designs for forest insect loss surveys in western United States. Berkeley, Calif. (Mar. 15, 1951.)
(U92) Hauge, O. J.
1925. Effect of climatic conditions on epidemics of *D. brevicomis* in yellow pine. Palo Alto, Calif., West. Div. News Letter. (Jan. 1, 1925.)
(U93) Hauke, Harold A.
1937. Further observations and studies on *Ips oregoni* in the Black Hills thinning areas—1936. Fort Collins, Colo. (Sept. 1, 1937.)
(U94) Hensill, George S.
1934. Mortality of *D. brevicomis* by radio waves. Berkeley, Calif. (Dec. 30, 1934.)

(U95) Hensill, George S.
1935. Summary of laboratory experiments and toxicity tests concerned with oil control of bark beetles. Berkeley, Calif. (Mar. 28, 1935.)
(U96) ———
1935. Some final field experiments on oil control of pine bark beetles, season of 1935. Berkeley, Calif. (Nov. 13, 1935.)
(U97) ———
1935. Review of oil control experiments on pine bark beetles. Berkeley, Calif. (Dec. 23, 1935.)
(U98) ———
1936. Some olfactory responses of the mountain pine beetle. Berkeley, Calif. (Jan. 10, 1936.)
(U99) Herbert, F. B.
1916. Biological notes on certain western species of the genus *Ips*. Los Gatos, Calif. (Dec. 1916.)
(U100) Hodgson, A. H.
1911. Reconnaissance report on representative sections infested with *Dendroctonus brevicomis* (western pine beetle) on Klamath National Forest. Yreka, Calif. (May 18, 1911.)
(U101) Jaenicke, A. J.
1920. Proceedings and recommendations of the 3rd Ashland Conf. on western forest insect problems, 1919. Ashland, Oreg. (Jan. 1920.)
(U102) ———
1921. Forest insect situation in southern Oregon and northern California. 1st Sup. Rpt. Portland, Oreg. (May 20, 1921.)
(U103) ———
1931. Logging of infested yellow pine as a method of *D. brevicomis* control. U.S. Forest Serv., Portland, Oreg. (Feb. 10, 1931.)
(U104) ———
1932. A new method of insect control (refers to decking logs with a caterpillar tractor). Portland, Oreg. (Apr. 30, 1932.)
(U105) ———
1935. Insect and drought conditions on the China Hat sale area. Portland, Oreg. (Feb. 19, 1935.)
(U106) ———
1936. A study of salvage of beetle-infested ponderosa pine in the China Hat and Fox Butte resale units on the Deschutes National Forest. Portland, Oreg. (May 16, 1936.)
(U107) Jeffrey, R. N.
1930. The concentration of certain sugars in the bark of western yellow pine as related to western pine beetle attraction. Berkeley, Calif. (Mar. 13, 1930.)
(U108) ———
1931. Preliminary report on the nutrition of the western pine beetle. Berkeley, Calif. (Mar. 1931.)
(U109) ———
1931. The concentration of certain sugars in the bark of western yellow pine in relation to western pine beetle attraction. Final rpt. Berkeley, Calif. (Aug. 31, 1931.)
(U110) Johnson, J. W.
1940. Field work dealing with *Matsucoccus* studies at the Hackamore and Halls Flat Laboratories, season of 1940. Berkeley, Calif. (Nov. 25, 1940.)
(U111) ———
1940. Composition studies of the 1940 season, Modoc National Forest. Berkeley, Calif. (Dec. 17, 1940.)
(U112) ———
1941. Memorandum describing root studies at the Hackamore field laboratory in the summer of 1940. Berkeley, Calif. (Jan. 3, 1941.)
(U113) ———
1941. Some variations in certain phases of the biology of *Melanophila californica* Van Dyke at Hackamore, Modoc County, Calif. Berkeley, Calif. (Apr. 29, 1941.)

(U114) Johnson, J. W.
1942. The occurrence of top-killed pines in the 1940 insect loss, Blacks Mountain Experimental Forest. Berkeley, Calif. (Feb. 26, 1942.)
(U115) ———
1942. The composition of insect infestations in ponderosa and Jeffrey pines, Lassen National Forest, seasons of 1940 and 1941. Berkeley, Calif. (Mar. 16, 1942.)
(U116) ———
1942. A preliminary study of the trapping of the western pine beetle in sawlogs at Blacks Mountain Experimental Forest. Berkeley, Calif. (May 19, 1942.)
(U117) ———
1942. Two-season emergence of *Melanophila californica* Van Dyke from materials collected at Hackamore, Modoc County, Calif., in the season of 1939. Berkeley, Calif. (July 25, 1942.)
(U118) ———
1942. Causes and effects of *Dendroctonus valens* attacks on reserve trees in areas treated by sanitation-salvage methods. Berkeley, Calif. (Aug. 7, 1942.)
(U119) ———
1942. Observations on the biology of *Dendroctonus valens* Lec., Blacks Mountain Experimental Forest, season of 1941. Berkeley, Calif. (Sept. 7, 1942.)
(U120) Johnson, P. C.
1932. Devils Garden extermination project, Modoc National Forest. Prog. rpt. Berkeley, Calif. (Jan. 1932.)
(U121) ———
1933. Devils Garden extermination project, Modoc National Forest. Prog. rpt. Berkeley, Calif. (Jan. 18, 1933.)
(U122) ———
1934. Devils Garden extermination project, Modoc National Forest. Discussion, 1932 infestation. Berkeley, Calif. (Feb. 2, 1934.)
(U123) ———
1935. Correction factors for use in estimating total seasonal bark beetle losses in California. Berkeley, Calif. (Feb. 5, 1935.)
(U124) ———
1942. Instructions for using roadside strips in the 1942 forest insect survey, California Region. Berkeley, Calif. (Sept. 19, 1942.)
(U125) ———
1944. Determining the bark beetle hazards of pine stands in northeastern California. Berkeley, Calif. (Jan. 27, 1944.)
(U126) ———
1946. Effect of sanitation-salvage cutting upon subsequent insect-caused pine mortality, Blacks Mountain Experimental Forest. Prog. rpt., 1937–43. Berkeley, Calif. (May 31, 1946.)
(U127) Keen, F. P.
1916. Notes on attraction of beetles, Lamb's Mine unit. Ashland, Oreg.
(U128) ———
1916. Notes on seasonal history and habits of *Ips confusus*, Lamb's Mine unit, project 15a. Ashland, Oreg.
(U129) ———
1917. Cruising manual for North Pacific states. Ashland, Oreg.
(U130) ———
1917. Seasonal history of *Dendroctonus brevicomis*, Lamb's Mine unit, project 15a. Ashland, Oreg. (Feb. 10, 1917.)
(U131) ———
1917. Flight habits of *Dendroctonus brevicomis*, Lamb's Mine unit, project 15a. Ashland, Oreg. (Feb. 17, 1917.)
(U132) ———
1917. Development of infested trees, Ashland area, Lamb's Mine unit, 1916. Ashland, Oreg. (Feb. 24, 1917.)
(U133) ———
1917. Quantitative analysis of infestation on Lamb's Mine unit. Ashland, Oreg. (Mar. 1917.)

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(U134) Keen, F. P.
1917. Notes on seasonal history of miscellaneous insects, Ashland areas, Lamb's Mine unit. Ashland, Oreg. (Mar. 31, 1917.)
(U135) ———
1923. Instruction to spotting crews, southern Oregon-northern California insect control project. 2d ed. Klamath Falls, Oreg. (Oct. 1, 1923.)
(U136) ———
1924. Some technical aspects of the southern Oregon-northern California pine beetle control project. Klamath Falls, Oreg. (Mar. 1, 1924.)
(U137) ———
1924. Memorandum of examination of insect conditions on timber sale areas on the North Warner Division, Modoc National Forest. Klamath Falls, Oreg. (Nov. 1924.)
(U138) ———
1925. Analysis of results of control, southern Oregon-northern California pine beetle control project, 1922–25. Stanford Univ., Calif. (Apr. 15, 1925.)
(U139) ———
1925. Statistical report of surveys, southern Oregon-northern California project, seasons of 1921, 1922, and 1923. Stanford Univ., Calif. (Apr. 15, 1925.)
(U140) ———
1927. Report of western pine beetle survey, Happy Camp-Lava Beds area, season of 1927. Stanford Univ., Calif. (Nov. 1927.)
(U141) ———
1927. Shooting bugs from the air. U.S. Dept. Agr. Bur. Ent. Western Forest Insect News, pp. 1–3. Stanford Univ., Calif. (Dec. 1, 1927.)
(U142) ———
1928. Analysis of brood statistics of the western pine beetle. Stanford Univ., Calif. (May 1, 1928.)
(U143) ———
1928. Western pine beetle extermination experiment, Timbered Mountain unit, Modoc National Forest. Stanford Univ., Calif. (Oct. 1928.)
(U144) ———
1928. Susceptibility of western yellow pines to bark beetle attack. Stanford Univ., Calif. (Feb. 1928.)
(U145) ———
1929. Work plan for the Devils Garden extermination experiment, season of 1929, Modoc National Forest. Stanford Univ., Calif. (Mar. 13, 1929.)
(U146) ———
1931. Estimating pine beetle losses during period of attack. Portland, Oreg. (Feb. 6, 1931.)
(U147) ———
1932. Windfalls as a cause of bark beetle epidemics. Portland, Oreg. (Dec. 1932.)
(U148) ———
1933. Memorandum for Mr. Clay Allen, U.S. Forest Service: data from ponderosa pine bark infested with western pine beetle and given electrical and oil treatments. Portland, Oreg. (May 6, 1933.)
(U149) ———
1933. Report of southern Oregon pine beetle surveys during season 1931, 1932. Stat. Rpt. 9, Portland, Oreg. (July 1933.)
(U150) ———
1933. The Ochoco-McKay Creek pine beetle control projects—analysis of results and recommendations for additional control work during fall of 1933. Portland, Oreg. (Oct. 9, 1933.)
(U151) ———
1935. Relative susceptibility of ponderosa pines to bark beetle attack. Portland, Oreg. (June 1935.)

(U152) Keen, F. P.
1939. Multiple correlation analysis of gross insect loss to hazard factors on Klamath Basin plots, Oreg. Portland, Oreg. (June 20, 1939.)
(U153) ———
1939. An approach to the problem of determining pine beetle hazard in ponderosa pine forests of Oregon and Washington. Portland, Oreg. (July 29, 1939.)
(U154) ———
1939. A preliminary analysis of pine beetle hazard conditions in the Klamath subregion, Oreg. Portland, Oreg. (July 31, 1939.)
(U155) ———
1940. Pine beetle control logging experiment of the Weyerhaeuser Timber Company, Bly district, Oreg. Portland, Oreg. (Nov. 13, 1940.)
(U156) ———
1941. Low temperature differentials in one forest drainage. Portland, Oreg. (June 25, 1941.)
(U157) ———
1941. A study of comparative growth rates of live and beetle-killed trees. Portland, Oreg. (Aug. 1941.)
(U158) ———
1941. Variance of growth rate for index trees. Portland, Oreg. (Aug. 22, 1941.)
(U159) ———
1941. First year's results of the pine beetle control logging experiment of the Weyerhaeuser Timber Company, Rail Glade area, Bly district, Oreg. Portland, Oreg. (Nov. 18, 1941.)
(U160) ———
1941. Results of risk marking on uncut check section, Meryl Springs unit, Bly district, Oreg. Portland, Oreg. (Nov. 19, 1941.)
(U161) ———
1941. A preliminary analysis of pine beetle hazard conditions in the Deschutes subregion. Portland, Oreg. (Dec. 10, 1941.)
(U162) ———
1942. Second year's results of the pine beetle control logging experiment of the Weyerhaeuser Timber Company, Rail Glade area, Bly district, Oreg. Portland, Oreg. (Nov. 7, 1942.)
(U163) ———
1943. The South Ice Cave fire. A study of effects of fire in ponderosa pine forests. Portland, Oreg. (July 30, 1943.)
(U164) ———
1949. Present bark beetle control policy for the pine forests of the Pacific Coast States. June 12, 1946. Berkeley, Calif. (Apr. 1, 1949.)
(U165) ———
1949. Experimental spraying of standing trees for bark beetle control in California. Berkeley, Calif. (May 6, 1949.)
(U166) ———
1954. Ponderosa pine tree characteristics indicative of high risk to pine beetle attack. U.S. Forest Serv. Calif. Forest and Range Expt. Sta. (Aug. 1954.)
(U167) ———
1954. Bark beetle hazard factors in ponderosa pine stands of eastern Oregon and Washington. U.S. Forest Serv. Calif. Forest and Range Expt. Sta. (Oct. 5, 1954.)
(U168) ———
1955. Thirteen years' results of a test of pine beetle control logging by the Weyerhaeuser Timber Company, Swede Cabin area, Bly district, Oreg., 1941–53. U.S. Forest Serv. Calif. Forest and Range Expt. Sta. (Jan. 1955.)
(U169) ———
1955. A progress report on insect mortality studies on cutover ponderosa pine lands. U.S. Forest Serv. Calif. Forest and Range Expt. Sta. (Jan. 12, 1955.)

(U170) Keen, F. P. and Beal, J. A.
1933. Low temperatures as a limiting factor in western pine beetle epidemics. Prog. rpt. 1. Portland, Oreg. (Apr. 20, 1933.)
(U171) ——— and Grant, R. C.
1941. Multiple correlation analyses of hazard factors associated with future insect loss. Portland, Oreg. (Aug. 26, 1941.)
(U172) ——— and Merriam, R. E.
1953. Analysis of area hazard factors associated with western pine beetle damage in ponderosa pine stands of eastern Oregon and Washington. Berkeley, Calif. (Mar. 18, 1953.)
(U173) ——— and Patterson, J. E.
1916. Reconnaissance and cruise of the Applegate area. Ashland, Oreg. (Mar. 24, 1916.)
(U174) McKenzie, H. L.
1940. A preliminary report on the scale *Matsucoccus bisetosus* Morrison as a possible cause of juvenile and mature ponderosa and Jeffrey pine decadence in the Pacific Northwest. Berkeley, Calif. (Jan. 30, 1940.)
(U175) ———
1942. A progress report on the *Matsucoccus* situation on mature ponderosa and Jeffrey pine in California. Berkeley, Calif. (Jan. 29, 1942.)
(U176) Miller, J. M.
1911. Memorandum to forest supervisor, Klamath National Forest re: Hodgson's reconnaissance report of May 18. Yreka, Calif. (June 3, 1911.)
(U177) ———
1918. Project 15a. Investigations of *Dendroctonus* beetles and methods of controlling them. Ashland, Oreg. (Feb. 1918.)
(U178) ———
1918. A quantitative study of the depredations by *Dendroctonus* beetles in the Rogue River, Applegate, and Klamath River watersheds. Prelim. rpt. Ashland, Oreg. (Feb. 1918.)
(U179) ———
1918. Flight habits of *Dendroctonus* bettles. Ashland, Oreg. (Feb. 1918.)
(U180) ———
1918. Entomological data from treated trees, Kaweah project. Ashland, Oreg. (Dec. 27, 1918.)
(U181) ———
1919. Studies of infestation, Marble Fork project, season of 1918. Ashland, Oreg. (Jan. 22, 1919.)
(U182) ———
1919. Bark counts of *Dendroctonus brevicomis* infestations. Memo. for Dr. A. D. Hopkins. Ashland, Oreg. (Feb. 8, 1919.)
(U183) ———
1919. Project 15a Data for 1917. Ashland, Oreg. (Mar. 15, 1919.)
(U184) ———
1920. The infestation unit (3d Ashland Conf.). Ashland, Oreg. (Jan. 1920.)
(U185) ———
1920. Mortality of broods of the western pine beetle in infested bark exposed to direct sunlight. Ashland, Oreg. (Feb. 27, 1920.)
(U186) ———
1921. First annual report, San Joaquin project. North Fork, Calif. (May 14, 1921.)
(U187) ———
1922. Proceedings of Forest Insect Conference, Berkeley, Calif. North Fork, Calif. (Feb. 1922.)
(U188) ———
1924. Pine beetle buried alive—survive. Western News Letter. North Fork, Calif. (Feb. 1924.)
(U189) ———
1924. The use of trap trees in the control of the western pine beetle. North Fork, Calif. (Nov. 18, 1924.)

(U190) Miller, J. M.
1924. Control of the western pine beetle on the San Joaquin project. Final rpt. North Fork, Calif. (Dec. 20, 1924.)
(U191) ———
1925. Summary of bark counts, North Fork station. North Fork, Calif.
(U192) ———
1926. Aerial photography as a method of mapping yellow pine areas to show losses caused by bark beetles. Stanford Univ., Calif. (June 18, 1926.)
(U193) ———
1926. Western pine beetle studies and experiments, Cascadel unit, North Fork, Calif., season of 1925. Stanford Univ., Calif. (June 28, 1926.)
(U194) ———
1927. Insect infestations on cutover lands in the vicinity of Loyalton, Tahoe National Forest. Stanford Univ., Calif. (Nov. 9, 1927.)
(U195) ———
1928. Oat Mountain flight experiment, San Joaquin project 1925. Stanford Univ., Calif. (Apr. 27, 1928.)
(U196) ———
1929. North Fork burn study. Final rpt. Stanford Univ., Calif. (Mar. 28, 1929.)
(U197) ———
1929. Some temperature points affecting the western pine beetle. Stanford Univ., Calif. (July 1, 1929.)
(U198) ———
1934. Effectiveness of pine beetle oil #21046R in relation to time at a constant temperature of 60° F. Berkeley, Calif. (May 15, 1934.)
(U199) ———
1943. Interrelations of insects and fires, North Fork Burn study. Sup. rept. Berkeley, Calif. (Feb. 15, 1943.)
(U200) ———
1943. Summary of parasites of *Dendroctonus brevicomis*. Berkeley, Calif. (Oct. 29, 1943.)
(U201) ———
1945. Summary of information on *Ips confusus* from notes and report files of the Forest Insect Laboratory, Berkeley, Calif. Berkeley, Calif. (Mar. 12, 1945.)
(U202) ——— Hopping, Ralph, and Jaenicke, A. J.
1917. California surveys of 1917. Ashland, Oreg. (Nov. 24, 1917.)
(U203) ——— Hopping, Ralph, and Jaenicke, A. J.
1920. Proposed control work on Sierra National Forest. Proc. 3d Ashland Conf. on western forest insect problems. Ashland, Oreg. (Jan. 1920.)
(U204) ——— and Patterson, J. E.
1919. Interrelation of forest fires and insects: Mistletoe, Siskiyou, and Chinquapin burns, Oregon. Ashland, Oreg. (May 7, 1919.)
(U205) ——— and Person, H. L.
1924. Factors contributing to lack of infestation in isolated groups of yellow pine in the lower Sierra below the pine belt. North Fork, Calif. (Mar. 5, 1924.)
(U206) ——— and Person, H. L.
1924. A quantitative study of *D. brevicomis* broods, their mortality, the effect of predators, and emergence periods. North Fork, Calif. (Apr. 6, 1924.)
(U207) ——— and Person, H. L.
1927. Western pine beetle flight study, San Joaquin project, 1924. Stanford Univ., Calif. (June 9, 1927.)
(U208) ——— and Struble, G. R.
1935. Critical low temperatures for the western pine and mountain pine beetles. Berkeley, Calif. (Feb. 28, 1935.)
(U209) ——— Struble, G. R., and Hall, R. C.
1944. Forest insect control and investigations, Sierra National Forest, 1909–43. Berkeley, Calif. (June 8, 1944.)

(U210) Mirov, N. T.
1928. A study of western yellow pine (*Pinus ponderosa*) as the host tree of *Dendroctonus brevicomis*. Berkeley, Calif. (Nov. 22, 1928.)
(U211) ———
1928. A preliminary study of attraction with the western pine beetle (*Dendroctonus brevicomis*). Berkeley, Calif. (Dec. 5, 1928.)
(U212) Moore, A. D.
1951. Investigations on the control of western pine beetles with toxic sprays—season of 1950. Berkeley, Calif. (June 29, 1951.)
(U213) ———
1953. Control of *Dendroctonus brevicomis* Lec. and *Ips confusus* (Lec.) with residual-type sprays, 1951. Berkeley, Calif. (Jan. 27 1953.)
(U214) Patterson, J. E.
1920. Development of individual broods of *Dendroctonus* beetles in Yosemite National Park, season of 1919. Ashland, Oreg. (Jan. 17, 1920.)
(U215) ———
1920. Experiments conducted in the Jenny Creek area, Oreg., during summer of 1920. Artificial attraction of *D. brevicomis* to living yellow pine trees and solar heat method of control of *D. brevicomis*. Ashland, Oreg. (Dec. 1920.)
(U216) ———
1922. Proceedings of Forest Insect Conference, Berkeley, Calif. (pp. 52–53). Berkeley, Calif. (Feb. 1922.)
(U217) ———
1922. Interrelations of forest fires and insects. Mistletoe and Siskiyou burns. Data for 1920. Ashland, Oreg. (Feb. 7, 1922.)
(U218) ———
1923. Statistics on *Dendroctonus brevicomis* in yellow pine in southern Oregon, 1914–23. Stanford Univ., Calif.
(U219) ———
1924. The first (1922), second (1923), third (1924), and final (1924) annual reports of the Antelope Creek control project. Stanford Univ., Calif. (Dec. 9, 1924).
(U220) ———
1924. Nature's feathered foresters. Western Div. News Letter. Stanford Univ., Calif. (Apr. 1924.)
(U221) ———
1924. Supplementary reports on bark beetle losses in the Rogue River area, project 15a. Includes ann. rpts. for 1921 through 1924. Ashland, Oreg. (Dec. 15, 1924.)
(U222) ———
1926. Report of insect conditions and control work carried out by the Long Bell Lumber Company in 1925 on the Reservation tract in Klamath County, Oreg. Stanford Univ., Calif. (Feb. 20, 1926.)
(U223) ———
1926. Bark beetle loss in Parker Mountain burn. Stanford Univ., Calif. (Apr. 16, 1926.)
(U224) ———
1927. Notes on the mountain pine beetle, *D. monticolae*, in lodgepole pine infestations, season of 1926. Stanford Univ., Calif. (Mar. 30, 1927.)
(U225) ———
1929. The Aspen Lake fire, Oregon. Report of bark beetle developments on the burned area and on adjacent pine stands subsequent to fire. Stanford Univ., Calif. (Mar. 21, 1929.)
(U226) ———
1934. Preliminary results of oil treatment of ponderosa pine infested with *D. brevicomis* and of sugar pine infested with *D. monticolae*. Berkeley, Calif. (Jan. 17, 1934.)
(U227) ———
1940. Chemical injection of green trees for rustic construction materials. Berkeley, Calif. (Apr. 26, 1940.)
(U228) ———
1942. Chemical injection of high-risk ponderosa pine trees. Prog. rpts. Berkeley, Calif. (May 8, 1941 and May 18, 1942.)

(U229) Patterson, J. E.
1946. Some results of chemical impregnation of beetle-susceptible ponderosa pines. Berkeley, Calif. (Apr. 15, 1946.)
(U230) ———
1949. Some experiments in the control of several western bark beetles by use of toxic sprays. 2d Prog. rpt., season of 1948. Berkeley, Calif. (Apr. 29, 1949.)
(U231) ———
1950. Some experiments in control of several western bark beetles by use of toxic sprays. Final rpt. Berkeley, Calif. (Apr. 26, 1950.)
(U232) Perry, Albert S.
1947. Preliminary investigations of the residual effect of DDT and other insecticides on the California five-spined engraver beetle, *Ips confusus* (Lec.) and the western pine beetle, *Dentroctonus brevicomis* Lec. Berkeley, Calif. (Sept. 25, 1947.)
(U233) Person, H. L.
1923. Preliminary studies on predacious insect enemies of *Dendroctonus brevicomis*. North Fork, Calif. (Apr. 12, 1923.)
(U234) ———
1923. Studies on the importance of insects breeding in yellow pine slash. North Fork, Calif. (Nov. 15, 1923.)
(U235) ———
1923. A study of the predacious insect enemies of western forest scolytids. North Fork, Calif.
(U236) ———
1924. Further studies on predacious enemies of *Dendroctonus brevicomis*. North Fork, Calif. (Apr. 7, 1924.)
(U237) ———
1926. Studies on tree selection by the western pine beetle. Stanford Univ., Calif. (Apr. 3, 1926.)
(U238) ———
1927. Western pine beetle studies, Cascadel unit, North Fork, Calif., season of 1926. Stanford Univ., Calif. (Mar. 14, 1927.)
(U239) ———
1928. The effectiveness of different western yellow pine "line" slash disposal methods in insect control. Stanford Univ., Calif. (Jan. 10, 1928.)
(U240) ———
1928. A study of the clerid *Thanasimus nigriventris* Lec. with notes on other insect enemies of the western pine beetle. Stanford Univ., Calif. (May 8, 1928.)
(U241) ———
1928. Report of western pine beetle studies of 1927, Cascadel unit, North Fork, Calif. Stanford Univ., Calif. (May 28, 1928.)
(U242) ———
1929. Sample plot studies of tree selection by the western pine beetle. Berkeley, Calif. (Jan. 15, 1929.)
(U243) ———
1929. Preliminary results of an experimental cutting on the Timber Mountain sample plot. Berkeley, Calif. (Feb. 19, 1929.)
(U244) ———
1929. Western pine beetle biological studies, Modoc National Forest, season of 1928. Berkeley, Calif. (June 1, 1929.)
(U245) ———
1930. Attraction studies with the western pine beetle, season of 1929. Berkeley, Calif. (Mar. 1, 1930.)
(U246) ———
1930. Biological control studies with the western pine beetle. Prog. rpt., 1929. Berkeley, Calif. (Apr. 7, 1930.)
(U247) ———
1930. Results of an experimental cutting on the Timber Mountain sample plot. Berkeley, Calif. (Nov. 1930.)
(U248) ———
1930. Studies in the biological control of the western pine beetle, *Dendroctonus brevicomis* Lec. Berkeley, Calif. (Nov. 30, 1930.)
(U249) ———
1930. Progress report on fire study trees, Sugar Hill fire. Berkeley, Calif. (Nov. 1930.)

(U250) Riggs, J. D.
1914. Brood count of *D. brevicomis* tree near Bray, California (letter to Dr. H. E. Burke). Placerville, Calif. (Jan. 31, 1914.)
(U251) Rust, H. J.
1927. Report on experiments conducted to determine the relationship of bark and air temperature. Coeur d'Alene, Idaho.
(U252) ———
1930. Relation of insectivorous birds to mortality of the mountain pine beetle during the flight period. Coeur d'Alene, Idaho. (Mar. 25, 1930.)
(U253) ———
1931. Role of ants, centipedes, and rodents destructive to broods of the mountain pine beetle exposed by the peeling method of control. Final rpt. Coeur d'Alene, Idaho. (Apr. 29, 1931.)
(U254) ———
1933. Final report on the study of the relation of fire injury to bark beetle attack in ponderosa pine, Tubbs Hill burn. Coeur d'Alene, Idaho. (Feb. 10, 1933.)
(U255) ———
1934. Artificial control of *Dendroctonus valens* by the use of carbon disulphide and orthodichlorobenzene. Coeur d'Alene, Idaho. (Aug. 17, 1934.)
(U256) ———
1935. Final report on the biology of *Ips oregoni* and associated insects of Idaho. Coeur d'Alene, Idaho. (Feb. 27, 1935.)
(U257) ———
1941. Rearing of *Melanophila californica* and *M. gentilis* at Coeur d'Alene Laboratory. Coeur d'Alene, Idaho. (Jan. 10, 1941.)
(U258) Salman, K. A.
1930. Memorandum concerning insect conditions—Cleveland National Forest, October 1930. Berkeley, Calif. (Nov. 6, 1930.)
(U259) ———
1931. Tentative outline and plans for the projected regional survey of forest insect infestations and trends, Region 5. Berkeley, Calif. (Jan. 1931.)
(U260) ———
1931. Devils Garden extermination project, Modoc National Forest. Berkeley, Calif. (Jan. 1931.)
(U261) ———
1932. Results of an experimental cutting in the Timber Mountain sample plot, Modoc National Forest. Prog. rpt. season of 1931. Berkeley, Calif. (Jan. 25, 1932.)
(U262) ———
1933. Field observations on mortality on western pine beetle due to freezing. Berkeley, Calif. (Jan. 12, 1933.)
(U263) ———
1933. Further tests of oil sprays to control the western pine and mountain pine beetles. Berkeley, Calif. (Aug. 12, 1933.)
(U264) ———
1934. Entomological phases of the 1933–34 Badger insect control projects, Modoc National Forest. Berkeley, Calif. (Apr. 20, 1934.)
(U265) ———
1934. An appraisal of results of the 1931 insect control projects in Modoc National Forest, Calif. Berkeley, Calif. (Apr. 30, 1934.)
(U266) ———
1934. An experiment in salvage cutting as a means of reducing forest insect depredations. Final rpt. Timber Mountain marking experiment. Berkeley, Calif. (Aug. 7, 1934.)
(U267) ———
1934. Devils Garden extermination project, Modoc National Forest. Final rpt. Berkeley, Calif. (Aug. 14, 1934.)
(U268) ———
1934. Larval stadia of the western pine beetle. Berkeley, Calif. (Dec. 4, 1934.)

(U269) Salman, K. A.
1935. A survey of forest insect infestations of cutover areas in California. Berkeley, Calif. (Jan 15, 1935.)
(U270) ———
1935. Life history studies of the western pine beetle, season of 1934. Berkeley, Calif. (Feb. 14, 1935.)
(U271) ———
1935. The composition of forest insect infestations in ponderosa pine as determined by stem analyses. Berkeley, Calif. (Mar. 30, 1935.)
(U272) ———
1936. Entomological results of the 1934 thinning operations, Region 5. Berkeley, Calif. (Jan. 10, 1936.)
(U273) ———
1936. Results of 1933 control projects in Modoc and Lassen National Forests. Berkeley, Calif. (Nov. 25, 1936.)
(U274) ———
1937. Reconnaissance of the 1936–37 winter mortality of forest insects in California. Berkeley, Calif. (May 26, 1937.)
(U275) ———
1937. The effects of low temperatures of January 1937 on forest insect infestations of the following season in Modoc National Forest, California. Berkeley, Calif. (Dec. 23, 1937.)
(U276) ———
1938. Susceptibility classification for ponderosa and Jeffrey pine, eastside forests of northeastern California. Sta. memo. Berkeley, Calif. (May 5, 1938.)
(U277) ———
1939. *Ips-D. brevicomis* outbreaks in northern California areas, season of 1938. Berkeley, Calif. (Apr. 27, 1939.)
(U278) ———
1940. Observations on risk changes—Blacks Mountain Experimental Forest—with comments by Dr. Willis Wagener. Berkeley, Calif. (June 13, 1940.)
(U279) ———
1940. A preliminary study of the diameter growth of ponderosa pine and some of its relations with risk and incipient infestations of the flathead borer (*Melanophila californica* Van Dyke). Berkeley, Calif. (Aug. 21, 1940.)
(U280) ———
1941. The development and practice of salvage and sanitation-salvage logging in the pine stands of northeastern California. Berkeley, Calif. (Aug. 18, 1941.)
(U281) ——— and Bacon, F. W.
1933. Timber Mountain experimental marking plots, Modoc National Forest. Berkeley, Calif. (Jan. 14, 1933.)
(U282) ——— and Bongberg, J. W.
1936. Results of further work on head measurements of the several larval stadia of the western pine beetle. Berkeley, Calif. (Feb. 10, 1936.)
(U283) ——— and Bongberg, J. W.
1936. A review of the results of some recent studies on the biology of the western pine beetle. Berkeley, Calif. (June 30, 1936.)
(U284) ——— and Bongberg, J. W.
1937. *Melanophila gentilis* Lec. and *M. californica* V.D. in ponderosa pine and Jeffrey pine: a review of published and unpublished notes. Berkeley, Calif. (Feb. 2, 1937.)
(U285) ——— and Johnson, P. C.
1936. Entomological phases of salvage logging projects. Berkeley, Calif. (Mar. 16, 1936.)
(U286) ——— and Johnson, P. C.
1937. The forest insect hazard inventory of the eastside forest areas. Prelim. rpt. on methods and their application. Berkeley, Calif. (Sept. 21, 1937.)

(U287) Salman, K. A. and Johnson, P. C.
1937. Forest insect hazard ratings for the Eagle Lake tracts of the Fruit Growers Supply Company and the Red River Lumber Company. Berkeley, Calif. (Dec. 7, 1937.)
(U288) ——— and Johnson, J. W.
1940. Studies on the movement of solutions through flathead-caused scars in the sapwood of ponderosa pine. Berkeley, Calif. (Mar. 28, 1940.)
(U289) ——— and McLees, K. C.
1938. The relation of minimum air temperatures and corresponding minimum temperatures in the bark of ponderosa pine trees at Hackamore, Calif. Berkeley, Calif. (Mar. 23, 1938.)
(U290) ——— and Wohletz, E. F.
1932. Sugar Hill fire study plots, Modoc National Forest. Berkeley, Calif. (Dec. 8, 1932.)
(U291) Show, S. B.
1920. Snake Lake light burning experiments. 1st Prog. rpt. U.S. Forest Serv., San Francisco, Calif. (May 11, 1920.)
(U292) Struble, G. R.
1928. A preliminary study of the life history and habits of the red turpentine beetle in western yellow pine. Stanford Univ., Calif. (Jan. 10, 1928.)
(U293) ———
1929. A preliminary report of some of the secondary coleoptera associated with *D. brevicomis*. Stanford Univ., Calif. (Jan. 1, 1929.)
(U294) ———
1930. Preliminary studies of the feeding habits of the adult western pine beetle. Berkeley, Calif. (Feb. 1, 1930.)
(U295) ———
1930. Memorandum on nutritional studies of western pine beetle larvae. Berkeley, Calif. (May 21, 1930.)
(U296) ———
1932. The fir engraver beetle. Prog. rpt. season of 1931. Berkeley, Calif. (Mar. 1, 1932.)
(U297) ———
1932. Cascadel tree selection plot, study of losses, and application of tree selection theory, season of 1931. Prog. rpt. Berkeley, Calif. (May 11, 1932.)
(U298) ———
1933. Preliminary results of oil treated ponderosa pine infested with *D. brevicomis* and *Melanophila gentilis*. Berkeley, Calif. (Dec. 13, 1933.)
(U299) ———
1934. Relation between temperature and effectiveness of pine bark oil formulae 21046r on *D. brevicomis* broods. Berkeley, Calif. (Mar. 20, 1934.)
(U300) ———
1934. Summary of Dinkey oil control project. Berkeley, Calif. (Oct. 5, 1934.)
(U301) ———
1937. "Deadline" as a protection against *Dendroctonus monticolae*. Berkeley, Calif. (Apr. 1, 1937.)
(U302) ———
1937. Variation in attack by the western pine beetle according to light intensity. Berkeley, Calif. (May 18, 1937.)
(U303) ———
1942. Cascadel tree selection plot, a study of tree selection by the western pine beetle. Final rpt. Berkeley, Calif. (Apr. 10, 1942.)
(U304) ———
1944. The mountain pine beetle as an associated insect of *Dendroctonus brevicomis*. Berkeley, Calif. (June 13, 1944.)
(U305) ———
1946. McLeod Flat blowdown in relation to subsequent *D. brevicomis* outbreak, Bass Lake unit. Berkeley, Calif. (Jan. 24, 1946.)

(U306) Struble, G. R.
1946. Possibilities of "goop" to control bark beetles under thick bark. Berkeley, Calif. (June 10, 1946.)
(U307) ———
1946. Slash breeding by *Ips* in relation to subsequent attack on living ponderosa pine. Prog. rpt. of Sierra studies, season of 1945. Berkeley, Calif. (Mar. 13, 1946.)
(U308) ———
1947. A study of factors in the development of *Ips* outbreaks. Prog. rpt. of Sierra studies, season of 1946. Berkeley, Calif. (Apr. 16, 1947.)
(U309) ———
1949. Biological and host factors in relation to *Ips* outbreaks in the southern Sierra subregion. Prog. rpt. season of 1947. Berkeley, Calif. (Jan. 14, 1949.)
(U310) ———
1949. A study in factors in the development of *Ips* outbreaks in the southern Sierra subregion, season of 1948. Berkeley, Calif. (May 2, 1949.)
(U311) ———
1950. A study of logging slash in relation to *Ips* breeding. Berkeley, Calif. (Apr. 20, 1950.)
(U312) ———
1950. Use of the helicopter as a spotting tool on insect control projects. Berkeley, Calif. (Mar. 20, 1950.)
(U313) ——— and Hall, R. C.
1950. Control of *Ips confusus* in ponderosa pine stands of the westside Sierra Nevada. Berkeley, Calif. (Oct. 23, 1950.)
(U314) ——— and Hensill, G. S.
1935. Oil control experiments against *D. brevicomis, D. monticolae*, and flatheads. Berkeley, Calif. (Jan. 8, 1935.)
(U315) Wagener, Willis W.
1930. Degrade from bluestain and other fungi in insect-attacked western yellow pine Modoc National Forest. Off. Forest Path., San Francisco, Calif. (Apr. 7, 1930.)
(U316) Wear, J. F.
1949. Aircraft operations in connection with studies of aerial spraying, aerial survey, and aerial photography. Prog. rpt. 1947–48 seasons. Portland, Oreg. (Jan. 26, 1949.)
(U317) Weaver, Harold.
1934. Memorandum on pine beetle control logging projects, Klamath Indian Reservation, Oreg. (Mar. 2, 1934.)
(U318) ———
1934. I.E.C.W. pine beetle control in the Pacific Northwest. (Dec. 6, 1934.)
(U319) ———
1935. Pine beetle control activities on Indian Reservations of the Pacific Northwest, October 1934 to May 1935. Emergency Conserv. Rpt. (July 1, 1935.)
(U320) ———
1940. The pine bark beetle situation on Indian Reservations of the Pacific Northwest.
(U321) West, Allen S., Jr.
1935. Preliminary report of aphis infestation of ponderosa pine on Prescott National Forest, Ariz., during the 1935 season. Berkeley, Calif. (Dec. 16, 1935.)
(U322) ———
1937. Low temperature tests with *Melanophila* larvae. Berkeley, Calif. (Feb. 23, 1937.)
(U323) ———
1937. *Melanophila* studies of the 1936 season at the Hackamore field laboratory. Berkeley, Callf. (Mar. 15, 1937.)
(U324) ———
1937. The nature of galleries formed by incipient stage larvae of *Melanophila californica* Van Dyke in ponderosa pine. Berkeley, Calif. (Apr. 20, 1937.)

(U325) West, Allen S., Jr.
1938. Progress report, *Melanophila* studies, 1937 season. Berkeley, Calif. (Apr. 20, 1938.)
(U326) ———
1938. Notes on species relations in infested ponderosa pines, Modoc National Forest, season of 1938. Berkeley, Calif. (Dec. 6, 1938.)
(U327) ———
1939. A brief survey of the effect of low temperatures in February 1939 on overwintering western pine beetle broods. Berkeley, Calif. (Mar. 27, 1939.)
(U328) ———
1939. Effect on nicotine sulfate injections in mature ponderosa pines. Berkeley, Calif. (Aug. 4, 1939.)
(U329) ———
1939. The injection of high risk ponderosa pines with copper sulfate. Berkeley, Calif. (Aug. 30, 1939.)
(U330) ———
1939. The California flathead borer, *Melanophila californica* Van Dyke, and the pine flathead borer, *M. gentilis* Lec.: a review of prog. of studies at Hackamore field lab. during the seasons of 1936–39. Berkeley, Calif. (Nov. 2, 1939.)
(U331) Whiteside, J. M.
1935. Temperature requirements for pupation of the western pine and mountain pine beetles. Berkeley, Calif. (May 20, 1935.)
(U332) ———
1941. Concerning the deterioration and salvage of insect-killed ponderosa pine trees. Portland, Oreg. (Mar. 1, 1941.)
(U333) ———
1941. Relation of cutting practice to bark beetle losses on ponderosa pine stands of the Silvies working circle, Malheur National Forest, Oreg., 1937–39. Portland, Oreg. (Aug. 12, 1941.)
(U334) ———
1945. Pine beetle hazard conditions on the Sisters' area of Deschutes National Forest. Portland, Oreg. (May 1945.)
(U335) ———
1946. Relation of cutting practice to bark beetle and other losses in ponderosa pine stands of the Silvies working circle, Malheur National Forest, Oreg., 1937–44. Portland, Oreg. (Nov. 1, 1946.)
(U336) ———
1948. Pine beetle hazard conditions on Warm Springs Indian Reservation in 1946. Portland, Oreg. (Jan. 30, 1948.)
(U337) ——— and Buckhorn, W. J.
1945. Pine beetle hazard conditions on the Snow Mountain area, Ochoco and Malheur National Forests. Portland, Oreg. (Oct. 17, 1945.)
(U338) Wygant, N. D.
1942. Studies of physical characteristics of high- and low-risk ponderosa pines, Blacks Mountain Experimental Forest, season of 1942. Berkeley, Calif. (May 26, 1942.)
(U339) ———
1942. Accuracy of appraising needle complement per twig and needle length on ponderosa pine. Berkeley, Calif. (June 24, 1942.)
(U340) Yuill, J. S.
1935. Critical low temperatures for the western pine and mountain pine beetles. 2d prog. rpt. of studies 1933–34. Berkeley, Calif. (May 31, 1935.)
(U341) ———
1935. Bark temperatures in ponderosa pine during attack by *Dendroctonus brevicomis*. Berkeley, Calif. (Sept. 10, 1935.)
(U342) ———
1936. Critical low temperatures for the western pine and mountain pine beetles. Memo. on lab. records, May to December 1935. Berkeley, Calif. (Jan. 13, 1936.)

(U343) Yuill, J. S.
1936. Critical low temperatures for the western pine and mountain pine beetles. Memo. on lab. records, January to April 1936. Berkeley, Calif. (Apr. 15, 1936.)
(U344) ———
1938. Relation of fat and moisture content to cold hardiness in larvae of *D. brevicomis* and *D. monticolae*. Berkeley, Calif. (Mar. 31, 1938.)
(U345) ———
1940. Preliminary tests of fumigants (methyl bromide) in bark beetle control, season of 1939. Berkeley, Calif. (Feb. 2, 1940.)
(U346) ———
1942. Studies on the biology of the western pine beetle, 1941 season. Berkeley, Calif. (Apr. 23, 1942.)

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